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Research Article

# Morphology and multigene phylogeny reveals five new species of Hydnaceae (Cantharellales, Basidiomycota) from China

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## Abstract

Wood-inhabiting fungi play a fundamental role in ecosystem processes, particularly in wood degradation and the recycling of organic matter. In this study, a new genus, *Clavuliella* **gen. nov.**, and five new species, viz. *Burgella albofarinacea* **sp. nov.**, *B. fissurata* **sp. nov.**, *Burgoa wumengshanensis* **sp. nov.**, *Clavuliella sinensis* **sp. nov.**, and *Sistotrema sinense* **sp. nov.**, are described from China and illustrated based on morphological characteristics and molecular phylogenetic analyses. Sequences of the ITS+nLSU genes were used for the phylogenetic analyses using Maximum Likelihood, Maximum Parsimony, and Bayesian Inference methods. The phylogram of the family Hydnaceae, based on the ITS+nLSU rDNA gene regions, included four genera; *Burgella*, *Burgoa*, *Clavuliella* and *Sistotrema.* The topology based on these sequences revealed that *Burgella albofarinacea* was closely related to *B. flavoparmeliae*, and *B. fissurata* was grouped with *B. lutea*. The taxon *Burgoa wumengshanensis* was sister to the clade that included *B. anomala* and *B. verzuoliana*. The species *Sistotrema sinense* was grouped closely with *S. brinkmannii* and *S. farinaceum.* All new taxa can be readily recognized by their macroscopic and anatomical characteristics. The five new species, closely related taxa in the phylogenetic tree, and morphologically similar species are discussed.

**Key words:** Asia, biodiversity, molecular systematics, taxonomy, wood-inhabiting fungi

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## Introduction

Fungi constitute an integral and valuable part of our natural ecosystem and play an essential ecological role in driving carbon cycling in forest soils, mediating mineral nutrition of plants, and alleviating carbon limitations (Chen et al. 2023a, b; Niego et al. 2023; Dong et al. 2024a; Yang et al. 2025). The wood-inhabiting fungal family Hydnaceae Chevall includes many variations of the fruiting body types within the order Cantharellales J. Schröt (Cai and Zhao 2023; Gao et al. 2024), in which it comprises many representative wood-inhabiting

fungi taxa, such as bulbil-shaped, hypochnoid, corticioid, odontoid, poroid, clavarioid, ramarioid, mucronelloid, cantharelloid, and hydnoid basidiomes with diverse hymenophoral and cystidial morphology (Uehling et al. 2012; Diederich et al. 2014; Gruhn et al. 2017; Masumoto and Degawa (2020); Lawrey et al. 2020; Bondartseva and Zmitrovich 2023; Cai and Zhao 2023; Gao et al. 2024).

The genus *Burgella* Diederich & Lawrey (Hydnaceae, Cantharellales), typified by *B. flavoparmeliae* Diederich & Lawrey, is characterized by the following features: conidia cylindrical, conidiophores short, hyphae hyaline, septate, straight, rarely branched or anastomosed. Agglomerations of bulbils gelatinous in appearance, almost coralloid, composed of irregularly shaped bulbils; bulbils externally and internally composed of irregular, roundish or elongate cells with clamped septa (Diederich and Lawrey 2007). Based on the MycoBank database (http://www.mycobank.org, accessed on 30 March 2025) and the Index Fungorum (http://www.indexfungorum.org, accessed on 30 March 2025), the genus *Burgella* has 2 registered species and intraspecies names (Diederich and Lawrey 2007). Previous studies have shown that *B. flavoparmeliae* and *Sistotrema oblongisporum* M.P. Christ. & Hauerslev were the sister group of the genus *Multiclavula* (Diederich and Lawrey 2007). The species *B. flavoparmeliae* was only distantly related to the type species of the genus *Burgoa* Goid., which appeared in a different place in the order Cantharellales, and the research revealed that *B. flavoparmeliae* should not be included in *Burgoa*, but instead placed in the new genus *Burgella* (Diederich and Lawrey 2007).

The genus *Burgoa*, typified by *B. verzuoliana* Goid. (Hydnaceae, Cantharellales, Agaricomycotina), was established by Goidŕnich to accommodate microfungi producing multicellular spore-like structures with differentiated peridial and internal cells, i.e. bulbils. Apart from the production of the bulbils, members of this genus were distinguished by the formation of clamp connections on their mycelium. This feature showed their affinity to members of Agaricomycotina, but their position within the order Cantharellales was recognised only recently (Diederich and Lawrey 2007; Koukol and Kubátová 2015; Kiyuna et al. 2015). The genus *Burgoa* is a peculiar microscopic basidiomycete not forming any basidiocarps in its life cycle. So far, this saprotroph has sporadically been found mainly on different woody substrates but the overall knowledge of its ecology and distribution remains sparse due to its rarity (Koukol and Kubátová 2015). Based on the MycoBank database (http://www.mycobank.org, accessed on 30 March 2025) and the Index Fungorum (http://www.indexfungorum.org, accessed on 30 March 2025), the genus *Burgoa* has 10 registered species and intraspecies names (Diederich and Lawrey 2007; Koukol and Kubátová 2015; Kiyuna et al. 2015).

*Clavulina* J. Schröt. (Hydnaceae, Cantharellales), with *Clavulina cristata* (Holmsk.) J. Schröt. as its type species, was established in 1888 (Schröter 1888; He et al. 2019). In China, 14 *Clavulina* species have been reported on the basis of morphological and molecular analyses, most of which are found in subtropical regions (Gao et al. 2024). In the present study, the new genus *Clavuliella* falls within Hydnaceae (Cantharellales) and is closely related to *Clavulina*.

The genus *Sistotrema* Fr. (Hydnaceae, Cantharellales, Agaricomycetes, Agaricomycotina, Basidiomycota), typified by *S. confluens* Pers., is a comparatively large genus belonging to the phylum Basidiomycota and is morphologically characterized by resupinate or pileate-stipitate, soft basidiomes, smooth, grandinioid, hydnoid, or poroid hymenophore with various characteristic textures (pellicular, membranaceous, or ceraceous), a monomitic hyphal system with

oily inclusions, urniform basidia, and smooth, thin-walled, basidiospores containing cytoplasmic oil droplets (Eriksson et al. 1984; Bernicchia and Gorjón 2010; Cai and Zhao 2023). Based on the MycoBank database (http://www.mycobank.org, accessed on 30 March 2025) and the Index Fungorum (http://www.indexfungorum.org, accessed 30 March 2025), the genus *Sistotrema* has 224 registered species and intraspecies names, however the actual number of recognized species is 111 (Eriksson et al. 1984; Bernicchia and Gorjón 2010; Sugawara et al. 2022; Cai and Zhao 2023).

In the present study, extensive morphological examinations, combined with analyses of multi-gene sequences data, support the introduction of a new genus and 4 new species of wood-inhabiting fungi. Descriptions and illustrations based on morphological characteristics are presented along with evidence from phylogenetic analyses.

## Materials and methods

### Morphology

Fresh basidiomata of the fungi growing on angiosperm branches were collected from the Dali, Dehong, and Zhaotong of Yunnan Province, and Guiyang of Guizhou Province, P.R. China. Specimens were dried in an electric food dehydrator at 40 °C (Dong et al. 2024b) then sealed and stored in an envelope and deposited in the Herbarium of the Southwest Forestry University (SWFC), Kunming, Yunnan Province, P.R. China. Macromorphological descriptions were based on field notes and photos captured in the field and lab. Colour terminology followed Petersen (1996). Micromorphological data were obtained from the dried specimens when observed under a light microscope following the previous study (Cai and Zhao 2023). The following abbreviations are used for the micro characteristic description: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB– = acyanophilous, IKI = Melzer's Reagent, IKI– = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), Q = variation in the L/W ratios between the specimens studied and n = a/b (number of spores (a) measured from given number (b) of specimens).

### Molecular phylogeny

The EZNA HP Fungal DNA Kit (Omega Biotechnologies Co., Ltd., Kunming, China) was used to extract DNA with some modifications from the dried specimens. The nuclear ribosomal ITS region was amplified with primers ITS5 and ITS4 (White et al. 1990). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, with a final extension of 72 °C for 10 mins. The nuclear nLSU region was amplified with primer pair LR0R and LR7 (Rehner and Samuels 1994). The PCR procedure for nLSU was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for 1 min and 72 °C for 1.5 mins with a final extension of 72 °C for 10 mins. The PCR procedure for ITS and nLSU followed a previous study (Zhao and Wu 2017). All newly generated sequences were deposited in NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/) (Table 1).

**Table 1.** Names, specimen numbers, references and corresponding GenBank accession numbers of the taxa used in this study.

| Species name | Specimen No. | GenBank accession No. | | Country | References |
|---|---|---|---|---|---|
| | | ITS | nLSU | | |
| *Bergerella atrofusca* | BR Berger 34240 | MN902070 | MN902070 | Austria | Lawrey et al. (2020) |
| *Bryoclavula phycophila* | Hiroshi:Bryoclavula4 | OQ791465 | OQ791464 | Japan | NCBI Database |
| *B. phycophila* | S-287-FB3 | LC544109 | – | Japan | Masumoto and Degawa (2020) |
| ***Burgella albofarinacea*** | **CLZhao 31820** | **PQ758751** | **PQ758759** | **China** | **Present study** |
| ***B. albofarinacea*** | **CLZhao 32468** | **PQ758754** | **PQ758762** | **China** | **Present study** |
| ***B. albofarinacea*** | **CLZhao 32026** | **PQ758753** | **PQ758761** | **China** | **Present study** |
| ***B. albofarinacea*** | **CLZhao 31855** | **PQ758752** | **PQ758760** | **China** | **Present study** |
| ***B. fissurata*** | **CLZhao 30212** | **PQ758749** | **PQ758757** | **China** | **Present study** |
| *B. flavoparmeliae* | Flakus 23513 | – | KC336074 | USA | Diederich et al. (2014) |
| *B. flavoparmeliae* | Buck 38682 | – | DQ915469 | Bolivia | Diederich et al. (2014) |
| *B. flavoparmeliae* | JL192-01 SV1 | OR471304 | – | USA | Swenie et al. (2023) |
| *B. flavoparmeliae* | JL192-01 SV2 | OR471305 | – | USA | Swenie et al. (2023) |
| *B. flavoparmeliae* | JL192-01 SV3 | OR471306 | – | USA | Swenie et al. (2023) |
| *B. flavoparmeliae* | JL192-01 SV4 | OR471307 | – | USA | Swenie et al. (2023) |
| *B. lutea* | Etayo 27623 | KC336076 | KC336075 | Bolivia | Diederich et al. (2014) |
| *Burgella* sp. | WS34_1_2_A_ As_10000 | LC631658 | – | Japan | Unpublished |
| *Burgella* sp. | HHB-19354 | MW740322 | – | New Zealand | Unpublished |
| *Burgella* sp. | HHB-19352 | MW740323 | – | New Zealand | Unpublished |
| *Burgoa anomala* | CBS 130.38 | AB972780 | – | Japan | Kiyuna et al. (2015) |
| ***B. wumengshanensis*** | **CLZhao 33227** | **PQ758755** | **–** | **China** | **Present study** |
| *B. verzuoliana* | CBS 131.38 | AB972781 | – | Italy | Kiyuna et al. (2015) |
| ***Clavuliella sinensis*** | **CLZhao 31231** | **PQ758750** | **PQ758758** | **China** | **Present study** |
| *Clavulina cristata* | EL95_97 | – | AY586648 | Sweden | Larsson et al. (2004) |
| *C. iris* | ML 5135C1 | MN028412 | MN028396 | Cyprus | Campo et al. (2023) |
| *C. minor* | B30912949 | OP738993 | OP737360 | China | Gao et al. (2024) |
| *C. minor* | B30912949 | OR149156 | OR145333 | China | Gao et al. (2024) |
| *C. parvispora* | FCME 27650 | MH542550 | MN049492 | Mexico | Gao et al. (2024) |
| *C. parvispora* | FCME 27657 | MH542549 | MN049491 | Mexico | Gao et al. (2024) |
| *C. samuelsii* | TENN065723 | JQ638712 | – | USA | Gao et al. (2024) |
| *C. samuelsii* | PDD:89881 | GU222317 | – | New Zealand | Gao et al. (2024) |
| *C. subrugosa* | TENN043395 | JQ638711 | – | USA | Gao et al. (2024) |
| *C. subrugosa* | TN43395 | JN228221 | JN228221 | New Zealand | Gao et al. (2024) |
| *C. sphaeropedunculata* | FCME 27661 | MH542560 | MK253716 | Mexico | Gao et al. (2024) |
| *C. sphaeropedunculata* | MEXU 28222 | MH542557 | MK253717 | Mexico | Gao et al. (2024) |
| *Hydnum albidum* | MB11-6024/2 | – | AY293186 | Thailand | Binder et al. (2005) |
| *H. albomagnum* | AFTOL-ID 471 | DQ218305 | AY700199 | USA | Masumoto and Degawa (2020) |
| *H. rufescens* | MB18-6024/1 | – | AY293187 | Panama | Binder et al. (2005) |
| *Minimedusa obcoronata* | CBS 120605 | GQ303278 | GQ303309 | USA | Diederich and Lawrey (2007) |
| *M. polyspora* | CBS:113.16 | – | MH866167 | USA | Vu et al. (2019) |
| *M. polyspora* | SH-Ecto-3 | – | MG833798 | China | NCBI Database |
| *Multiclavula caput-serpentis* | KaiR699 | MW386064 | MW369074 | Japan | Reschke et al. (2021) |
| *M. corynoides* | Lutzoni 930804-2 | U66440 | U66440 | USA | Lutzoni (1997) |
| *M. mucida* | AFTOL-ID 1130 | DQ521417 | AY885163 | Switzerland | Masumoto and Degawa (2020) |
| *M. petricola* | NBRC 114399 | LC516464 | LC516465 | USA | Masumoto and Degawa (2020) |
| *M. vernalis* | Lutzoni 930806-1 | U66439 | U66439 | USA | Lutzoni (1997) |

| Species name | Specimen No. | GenBank accession No. | | Country | References |
|---|---|---|---|---|---|
| | | ITS | nLSU | | |
| *Neoburgoa freyi* | JL596-16 | KX423755 | KX423755 | Vietnam | Lawrey et al. (2016) |
| *N. freyi* | EZ4455 | OR471314 | OR471068 | Canada | Swenie et al. (2023) |
| *Platygloea disciformis* | AFTOL-ID 710 | DQ234556 | AY629314 | USA | Sugawara et al. (2022) |
| *Rogersiomyces malaysianus* | LE-BIN 3507 | KT779285 | – | Poland | Psurtseva et al. (2016) |
| *Sistotrema confluens* | FCUG 298 | – | DQ898711 | Canada | Moncalvo et al. (2006) |
| *S. confluens* | AFTOL-ID 613 | DQ267125 | AY647214 | Canada | Masumoto and Degawa (2020) |
| *S. adnatum* | FCUG 700 | – | DQ898699 | Sweden | Moncalvo et al. (2006) |
| *S. adnatum* | GB700 | OR464426 | OR460895 | Sweden | Swenie et al. (2023) |
| *S. alboluteum* | TAA167982 | – | AY586713 | Canada | Larsson et al. (2004) |
| *S. alboluteum* | TAA180259 | – | AJ606042 | Sweden | Nilsson et al. (2006) |
| *S. albopallescens* | KHL11070 | – | AM259210 | Canada | Nilsson et al. (2006) |
| *S. athelioides* | FCUG 701 | – | DQ898700 | Japan | Moncalvo et al. (2006) |
| *S. brinkmannii* | NH11412 | – | AF506473 | Sweden | Larsson et al. (2004) |
| *S. biggsiae* | FCUG 782 | – | DQ898697 | Sweden | Moncalvo et al. (2006) |
| *S. chloroporum* | TUMH 64399 | NR178117 | LC642057 | Sweden | Sugawara et al. (2022) |
| *S. citriforme* | KHL15898 | KF218962 | KF218962 | Sweden | Kotiranta and Larsson (2013) |
| *S. coroniferum* | GB-BN-2 | – | AM259215 | Canada | Nilsson et al. (2006) |
| *S. coroniferum* | KH Larsson s.n. | KF218968 | KF218968 | Netherlands | Kotiranta and Larsson (2013) |
| *S. coronilla* | NH7598 | – | AF506475 | USA | Larsson et al. (2004) |
| *S. efibulatum* | FCUG 1175 | – | DQ898696 | Canada | Moncalvo et al. (2006) |
| *S. epiphyllum* | CBS H-21517 | NR155795 | – | Canada | NCBI Database |
| *S. eximum* | Thorn429 | – | AF393076 | Finland | Binder and Hibbett (2002) |
| *S. eximum* | CBS:531.91 | MH862275 | MH873956 | Japan | Vu et al. (2019) |
| *S. farinaceum* | FCUG 659 | – | DQ898707 | Japan | Moncalvo et al. (2006) |
| *S. farinaceum* | HK23176 | KF218963 | KF218963 | Australia | Kotiranta and Larsson (2013) |
| *S. flavorhizomorphae* | TUMH:64401 | LC642038 | LC642059 | Finland | Sugawara et al. (2022) |
| *S. flavorhizomorphae* | TUMH:64402 | LC642040 | LC642060 | Sweden | Sugawara et al. (2022) |
| *S. hypogaeum* | CBS 394.63 | MH858314 | MH869926 | Finland | Vu et al. (2019) |
| *S. luteoviride* | H HK23176 | NR158892 | – | Sweden | Kotiranta and Larsson (2013) |
| *S. muscicola* | KHL8791 | – | AF506474 | Canada | Larsson et al. (2004) |
| *S. muscicola* | KHL 11721 | – | AJ606040 | USA | Nilsson et al. (2006) |
| *S. oblongisporum* | KHL 14077 | – | KF218970 | Spain | Kotiranta and Larsson (2013) |
| *S. octosporum* | FCUG 2822 | – | DQ898698 | USA | Moncalvo et al. (2006) |
| *S. octosporum* | CBS:126038 | MH864053 | MH875510 | Finland | Vu et al. (2019) |
| *S. pistilliferum* | EL 28/10 | KF218964 | KF218964 | Canada | Kotiranta and Larsson (2013) |
| *S. raduloides* | AFTOL-ID 619 | – | AY647213 | Sweden | Masumoto and Degawa (2020) |
| *S. raduloides* | LR 44004 | KF218969 | KF218969 | USA | Kotiranta and Larsson (2013) |
| *S. resinicystidium* | FCUG 2188 | – | DQ898708 | China | Moncalvo et al. (2006) |
| *S. sernanderi* | GB-BN-4 | – | AM259219 | China | Nilsson et al. (2006) |
| *S. sernanderi* | PUL:F24593 | MW448599 | – | China | NCBI Database |
| ***S. sinense*** | **CLZhao 24876** | **PQ758748** | **PQ758756** | **China** | **Present study** |
| *S. subconfluens* | Dai 12577 | JX076812 | JX076810 | China | Zhou and Qin (2013) |
| *S. subconfluens* | Dai 12578 | – | JX076811 | Sweden | Zhou and Qin (2013) |
| *S. yunnanense* | CLZhao 7357 | ON817194 | ON810362 | USA | Cai and Zhao (2023) |
| *S. yunnanense* | CLZhao 7395 | ON817195 | ON810363 | UK | Cai and Zhao (2023) |
| *S. brinkmannii* | NH11412 | – | AF506473 | Thailand | Larsson et al. (2004) |
| *Sistotremella perpusilla* | CBS 126048 | MH864061 | MH875516 | USA | Vu et al. (2019) |
| *S. perpusilla* | HFRG EJ210404 | OL828790 | – | Panama | NCBI Database |

The sequences were aligned in MAFFT version 7 (Katoh et al. 2019) using the G-INS-i strategy. The alignment was adjusted manually using AliView version 1.27 (Larsson 2014). The sequence alignments were deposited in TreeBase (https://treebase.org/treebase-web/home.html;jsessionid=4359D218F4D60336C2A9F7EB7D135CCD) (ID 32177 (Fig. 1)). The sequence alignments were deposited in TreeBase (https://treebase.org/treebase-web/home.html;jsessionid=4359D218F4D60336C2A9F7EB7D135CCD) (ID 32178 (Fig. 2)). Sequences of *Platygloea disciformis* (Fr.) Neuhoff retrieved from GenBank were used as the outgroup in the ITS+nLSU analysis (Figs 1, 2; Sugawara et al. 2022).

Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) analyses were applied to the combined three datasets following a previous study (Zhao and Wu 2017). All characters were equally weighted and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1,000 random sequence additions. Max trees were set to 5,000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using bootstrap (BT) analysis with 1,000 pseudo replicates (Felsenstein 1985). Descriptive tree statistics - tree length (TL), composite consistency index (CI), composite retention index (RI), composite rescaled consistency index (RC) and composite homoplasy index (HI) – were calculated for each maximum parsimonious tree generated. The combined dataset was also analysed using Maximum Likelihood (ML) in RAxML-HPC2 through the CIPRES Science Gateway (Miller et al. 2012). Branch support (BS) for the ML analysis was determined by 1,000 bootstrap pseudo replicates.

MrModelTest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each dataset for the purposes of Bayesian Inference (BI) which was performed using MrBayes 3.2.7a with a GTR+I+G model of DNA substitution and a gamma distribution rate variation across sites (Ronquist et al. 2012). A total of four Markov chains were run for two runs from random starting trees for 2 million generations for ITS+nLSU (Fig. 1) and 2 million generations for ITS+nLSU (Fig. 2) with trees and parameters sampled every 1,000 generations. The first quarter of all the generations were discarded as burn-in. A majority rule consensus tree was computed from the remaining trees. Branches were considered as significantly supported if they received a Maximum Likelihood bootstrap support value (BS) of ≥ 70%, a maximum parsimony bootstrap support value (BT) of ≥ 70%, or a Bayesian posterior probability (BPP) of ≥ 0.95.

## Results

### Molecular phylogeny

*Burgella albofarinacea* BLASTN homology search using the ITS nucleotide sequence indicated that the sequence had 87% identity with the sequence as OR471304, named *Burgella flavoparmeliae* from the NCBI culture collection (551/635 bp); the nLSU sequence had 98% identity with the sequence as DQ915469, named *B. flavoparmeliae* from the NCBI culture collection (1294/1323 bp). *Burgella fissurata* BLASTN homology search using the ITS nucleotide sequence indicated that the sequence had 88% identity with the sequence as OR471304, named *B. flavoparmeliae* from the NCBI culture collection (553/627 bp); the nLSU sequence had 98% identity with the sequence

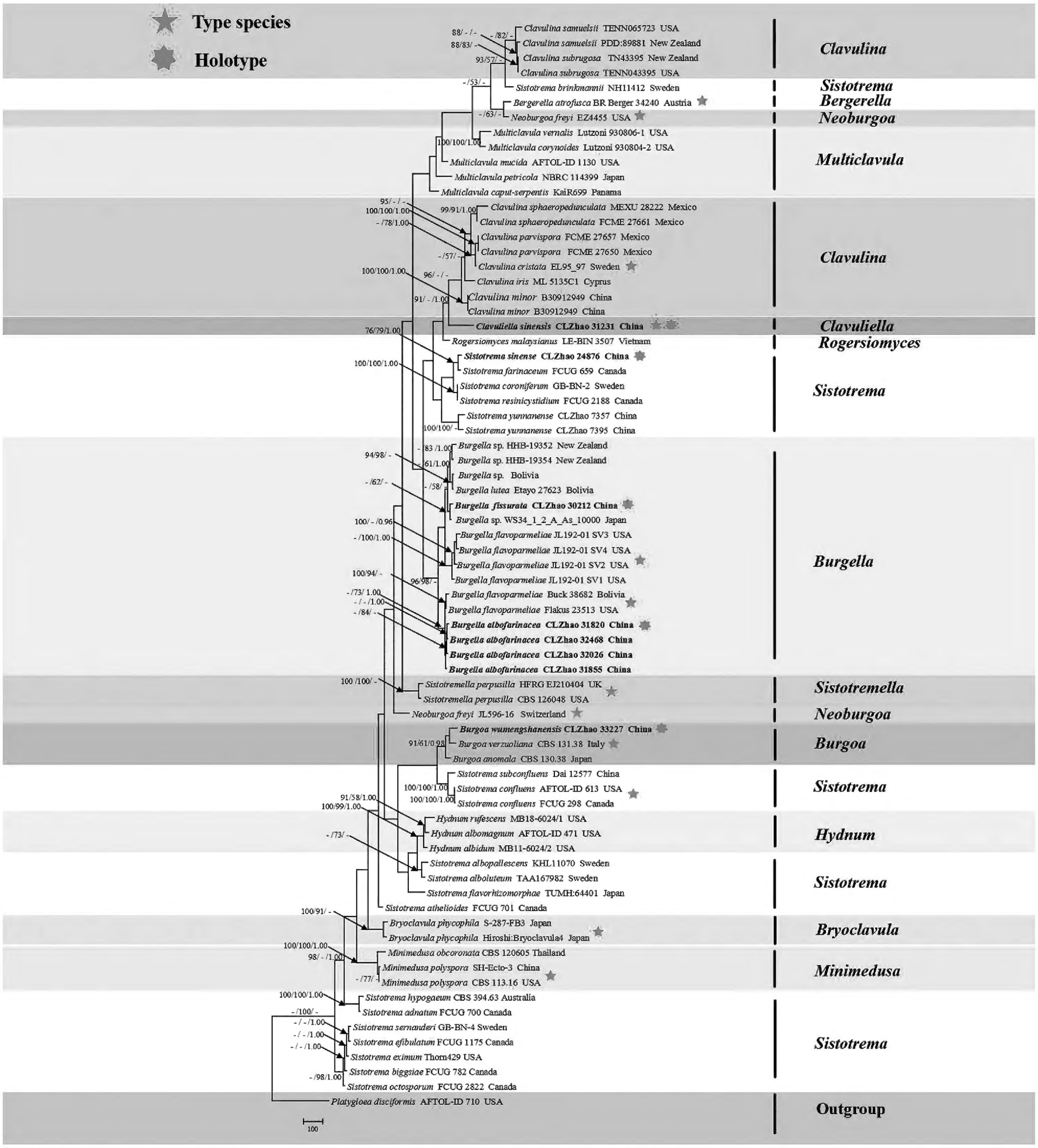


**Figure 1.** Maximum Parsimony strict consensus tree illustrating the phylogeny of four new species and a new genus within Hydnaceae, based on ITS+nLSU sequences. Branches are labelled with Maximum Likelihood bootstrap values ≥ 70%, parsimony bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 0.95, respectively.

as DQ915469, named *B. flavoparmeliae* from the NCBI culture collection (1290/1319 bp). *Burgoa wumengshanensis* BLASTN homology search using the ITS nucleotide sequence indicated that the sequence had 83% identity with the sequence as AB972780, named *Burgella flavoparmeliae* from the CBS culture collection (532/643 bp). *Clavuliella sinensis* BLASTN homology search using the ITS nucleotide sequence indicated that the sequence had 88% identity with the sequence as MT196962, named *Clavulina castaneipes* (G.F. Atk.) Corner. from the NCBI culture collection (602/688 bp); the nLSU sequence had

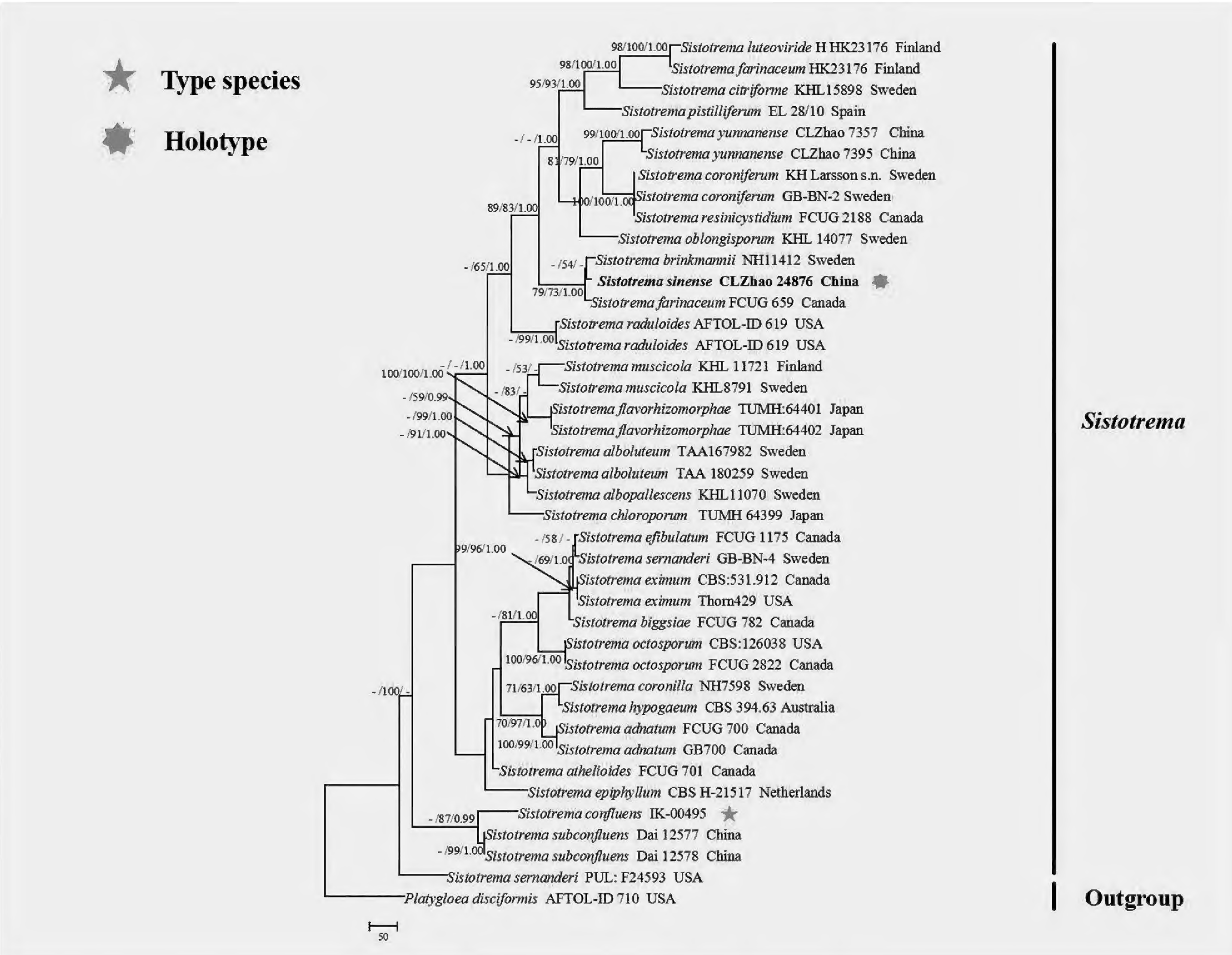


**Figure 2.** Maximum parsimony strict consensus tree illustrating the phylogeny of the one new species and related species in *Sistotrema*, based on ITS+nLSU sequences. Branches are labelled with Maximum Likelihood bootstrap values > 70%, parsimony bootstrap values > 50% and Bayesian posterior probabilities > 0.95, respectively.

96% identity with the sequence as OM942737, named *C. iris* from the NCBI culture collection (1281/1338 bp). *Sistotrema sinense* BLASTN homology search using the ITS nucleotide sequence indicated that the sequence had 81% identity with the sequence as OM100765, named *S. coroniferum* (Höhn. & Litsch.) Donk from the NCBI culture collection (541/669 bp); the nLSU sequence had 99% identity with the sequence as OR460882, named *S. brinkmannii* (Bres.) J. Erikss. from the NCBI culture collection (1324/1340 bp).

The ITS+nLSU dataset (Fig. 1) comprised sequences from 55 fungal specimens representing 73 taxa. The dataset had an aligned length of 3499 characters, of which 2000 characters were constant, 546 were variable and parsimony-uninformative, and 953 were parsimony-informative. Maximum parsimony analysis yielded 6 equally parsimonious trees (TL = 5747, CI = 0.4047, HI = 0.5953, RI = 0.5604 and RC = 0.2268). The best model of nucleotide evolution for the ITS+nLSU dataset estimated and applied in the Bayesian analysis was found to be GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as in the MP analysis. The Bayesian analysis had an average standard deviation of split frequencies = 0.207165 (BI) and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 362.5. The phylogram, based on the ITS+nLSU rDNA gene regions (Fig. 1), included five genera, viz. *Burgella*,

*Burgoa*, *Clavuliella* and *Sistotrema*, within the family Hydnaceae (Cantharellales, Agaricomycetes). The phylogenetic tree (Fig. 1) inferred from the ITS and nLSU sequences highlighted that the two new species were grouped into the genus *Burgella*, in which *B. albofarinacea* was closely related to *B. flavoparmeliae*, and *B. fissurata* was grouped with *B. lutea* Diederich, Capdet, A.I. Romero & Etayo. The phylogram based on the ITS and nLSU data (Fig. 1) showed that *Burgoa wumengshanensis* was clustered into the genus *Burgoa*, in which it was closely related to *B. anomala* (Hotson) Goid. and *B. verzuoliana* Goid. The phylogram based on the ITS+nLSU rDNA gene regions (Fig. 1), included one new species, viz. *Sistotrema sinense*, in which it was grouped into the genus *Sistotrema*.

The ITS+nLSU dataset (Fig. 2) comprised sequences from 30 fungal specimens representing 40 taxa. The dataset had an aligned length of 2031 characters, of which 1085 characters were constant, 365 were variable and parsimony-uninformative, and 581 were parsimony-informative. Maximum parsimony analysis yielded 12 equally parsimonious trees (TL = 2690, CI = 0.5487, HI = 0.4513, RI = 0.5550 and RC = 0.3045). The best model of nucleotide evolution for the ITS+nLSU dataset estimated and applied in the Bayesian analysis was found to be GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as in the MP analysis. The Bayesian analysis had an average standard deviation of split frequencies = 0.005023 (BI) and the effective sample size (ESS) across the two runs is double the average ESS (avg. ESS) = 813.5. The phylogenetic tree (Fig. 2), inferred from the ITS+nLSU sequences, highlighted that *Sistotrema sinense* was grouped closely with *S. brinkmannii* (Bres.) J. Erikss. and *S. farinaceum* Hallenb.

## Taxonomy

***Burgella albofarinacea* Q. Zhou & C.L. Zhao, sp. nov.**
MycoBank No: 857296
Figs 3–5

**Holotype.** China • Yunnan Province, Zhaotong, Yiliang County, Longhai Town, Jianfeng mountain, GPS coordinates: 27°76'N, 104°37'E, altitude: 1777 m asl., on the fallen branch of angiosperm, leg. C.L. Zhao, 26 August 2023, CL Zhao 31820 (SWFC).

**Etymology.** *albofarinacea* (Lat.): refers to the albicans and farinaceous hymenophore of the type specimens.

**Description.** Basidiomata annual, resupinate, adnate, pellicular, coriaceous, without odor or taste when fresh, up to 11.5 cm long, 2 cm wide, 50–100 µm thick. Hymenial surface smooth, farinaceous, white when fresh and drying, cracked. Sterile margin thin, white, thinning out, up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, sometimes with oily contents, colorless, slightly thick-walled, frequently branched, interwoven, 3.5–5.5 µm in diameter; IKI–, CB–, tissues unchanged in KOH.

Cystidia and cystidioles absent. Basidia suburniform to urniform, slightly thick-walled, with 8 sterigmata and a basal clamp connection, 10.5–22 × 3.5–7 µm; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores ellipsoid to allantoid, colorless, thin-walled, smooth, with oil drop, IKI–, CB–, (4–)4.5–6.5(–7) × 2–4 µm, L = 5.34 µm, W = 2.83 µm, Q = 1.79–1.97 µm (n = 120/4).

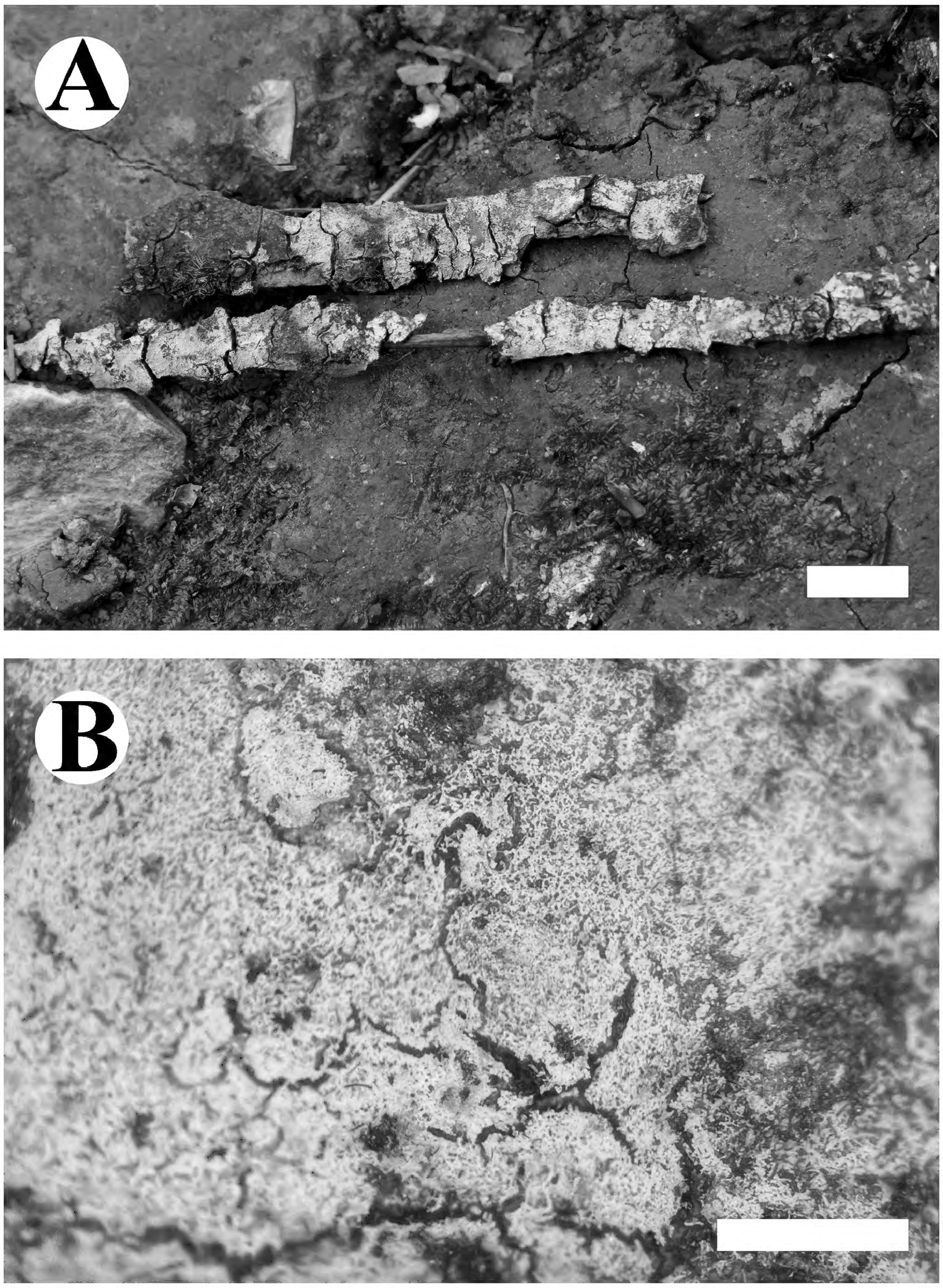


**Figure 3.** Basidiomata of *Burgella albofarinacea* (holotype). Scale bars: 1 cm (**A**); 1 mm (**B**).

**Additional specimens examined (paratypes).** China • Yunnan Province, Zhaotong, Yiliang County, Longan Town, GPS coordinates: 27°73'N, 104°16'E, altitude: 1550 m asl., on the fallen branch of angiosperm, leg. C.L. Zhao, 27 August 2023, CLZhao 32026, CLZhao 31855 (SWFC) • Zhaotong, Yiliang County, Xiaocaoba Town, GPS coordinates: 27°26'N, 104°26'E, altitude: 2225 m asl., on the fallen branch of angiosperm, leg. C.L. Zhao, 28 August 2023, CLZhao 32468 (SWFC).

***Burgella fissurata*** **Q. Zhou & C.L. Zhao, sp. nov.**
MycoBank No: 857297
Figs 6–8

**Holotype.** China • Yunnan Province: Dehong, Yingjiang County, Tongbiguan provincial nature reserve, GPS coordinates: 24°30'N, 097°30'E, altitude: 1300 m asl., on the fallen branch of angiosperm, leg. C.L. Zhao, 19 July 2023, CLZhao 30212 (SWFC).

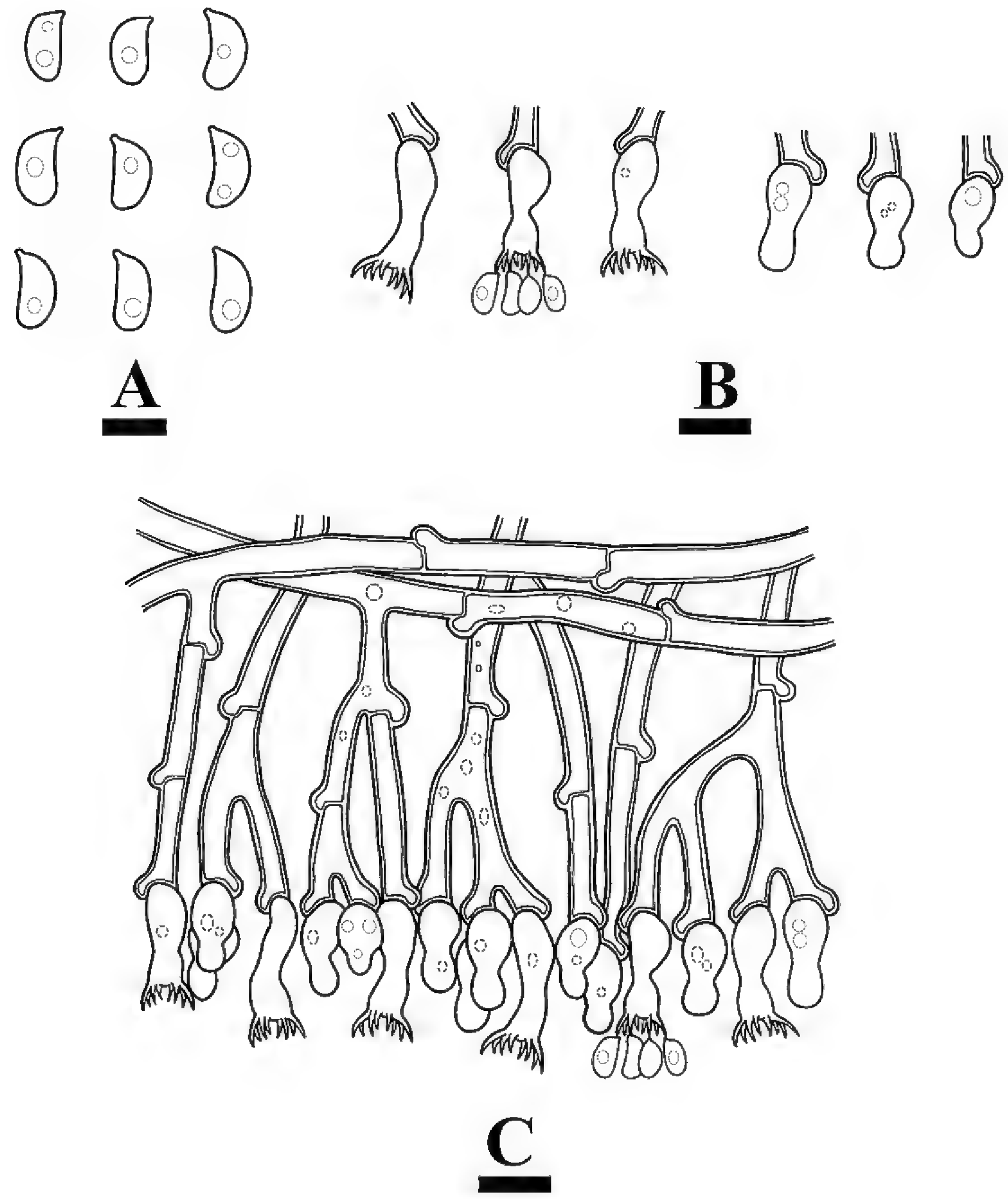


**Figure 4.** Microscopic structures of *Burgella albofarinacea* (holotype): basidiospores (**A**), basidia and basidioles (**B**), a section of hymenium (**C**). Scale bars: 5 µm (**A**); 10 µm (**B, C**).

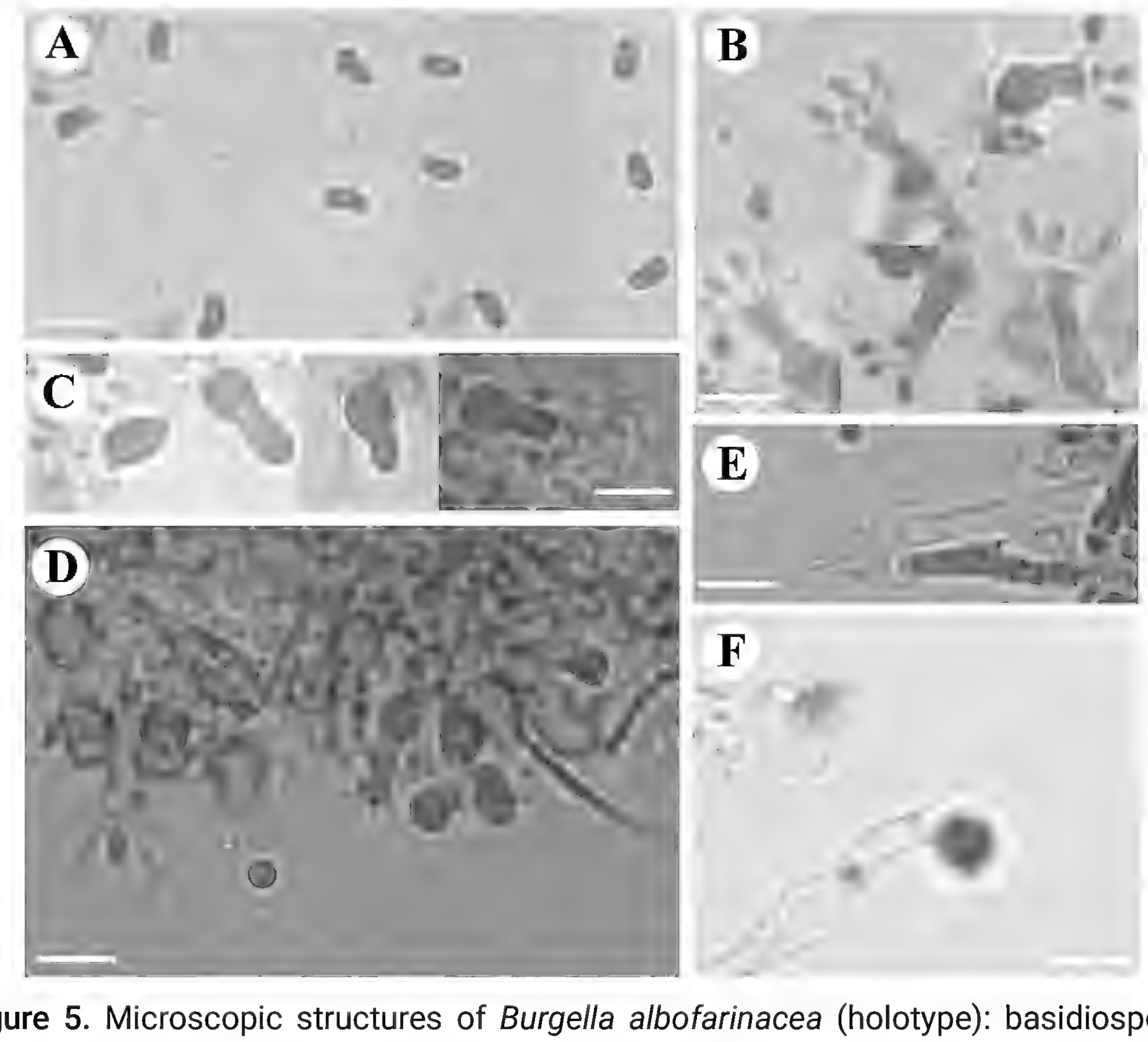


**Figure 5.** Microscopic structures of *Burgella albofarinacea* (holotype): basidiospores (**A**), basidia (**B**), basidioles (**C**), a section of hymenium (**D**), generative hyphae (**E, F**). Scale bars: 10 µm (**A–F**).

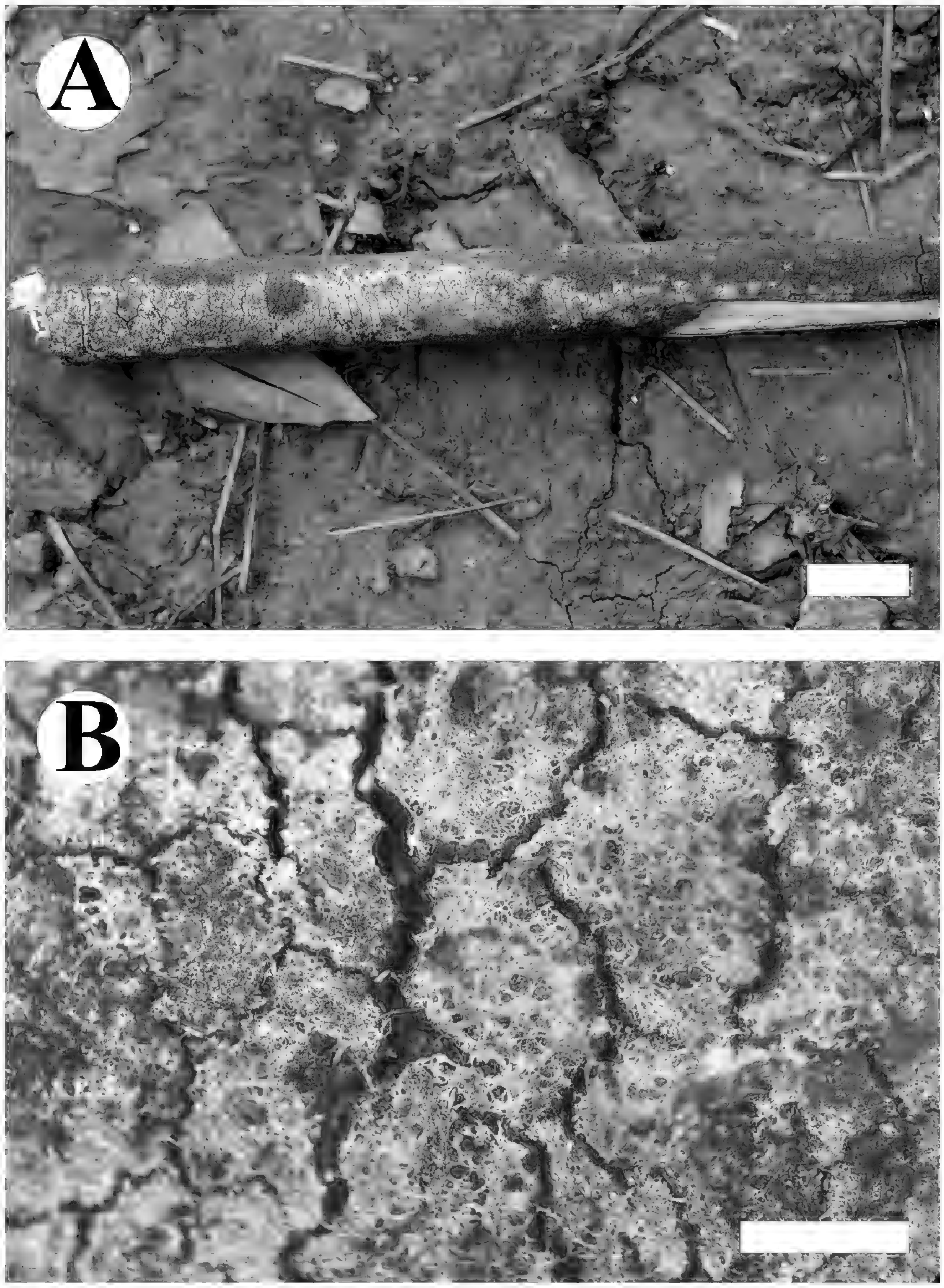


**Figure 6.** Basidiomata of *Burgella fissurata* (holotype). Scale bars: 1 cm (**A**); 1 mm (**B**).

**Etymology.** *fissurata* (Lat.): refers to the cracking hymenial surface of the type specimens.

**Description.** Basidiomata annual, resupinate, adnate, pruinose, hypochnoid, without odor or taste when fresh, up to 10.2 cm long, 1 cm wide, 50–100 μm thick. Hymenial surface smooth, cracked, white when fresh, turning to pale cream upon drying. Sterile margin thin, white, thinning out, up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, colorless, thin-walled, frequently branched, interwoven, 2–4 μm in diameter; IKI–, CB–, tissues unchanged in KOH.

Cystidia umbrella-shaped, colorless, thin-walled, smooth, 5.5–10 × 4–6 μm; cystidioles absent. Basidia urniform, with a median constriction, thin-walled, with 4 sterigmata and a basal clamp connection, 6–11.5 × 2–4.5 μm; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores narrowly ellipsoid, colorless, thin-walled, smooth, IKI–, CB–, (2.5–)3–4 × 1–2 μm, L = 3.36 μm, W = 1.63 μm, Q = 2.06 μm (n = 30/1).

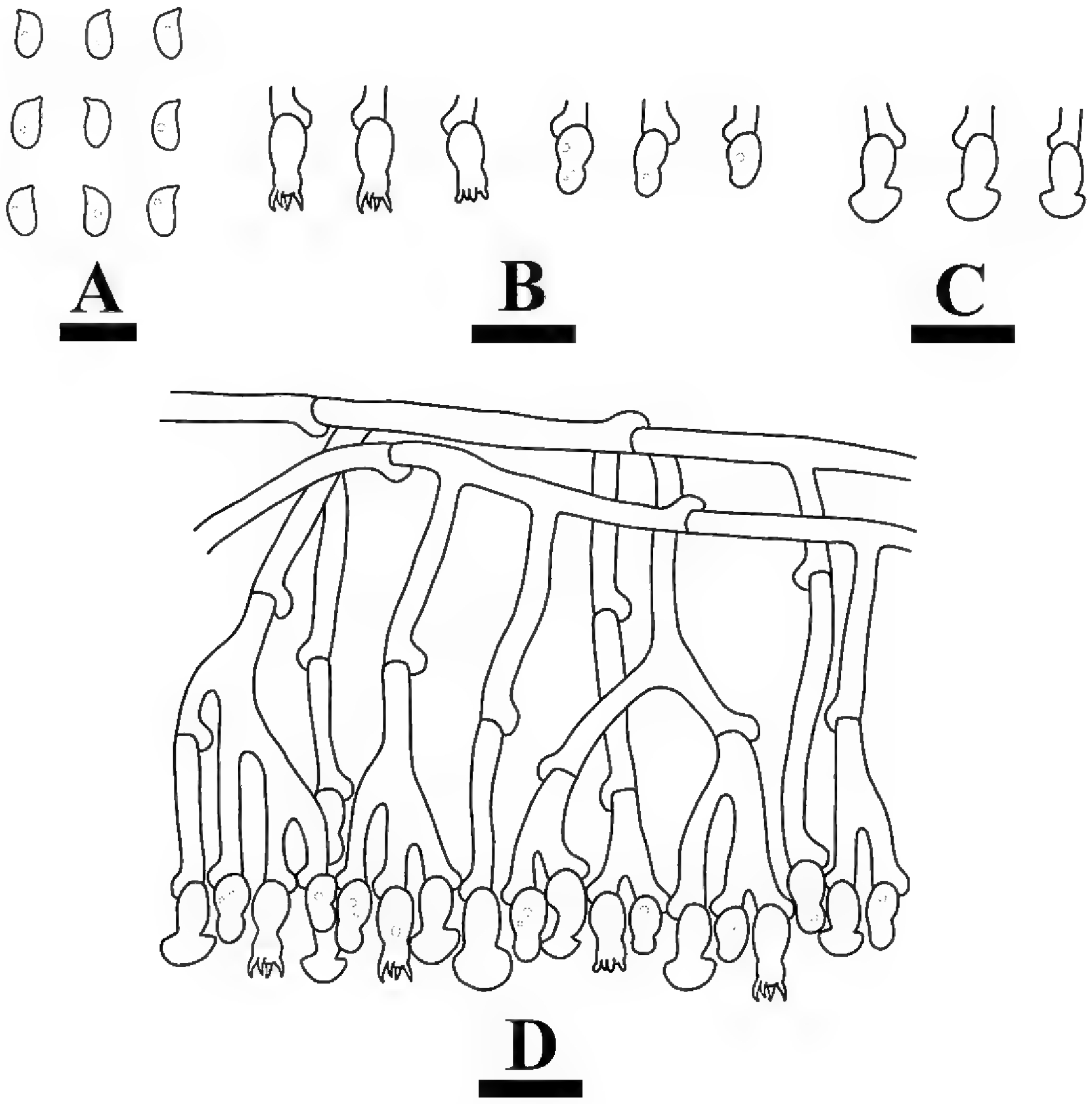


Figure 7. Microscopic structures of *Burgella fissurata* (holotype): basidiospores (**A**), basidia and basidioles (**B**), umbrella-shaped cystidia (**C**), a section of hymenium (**D**). Scale bars: 5 μm (**A**); 10 μm (**B, C**).

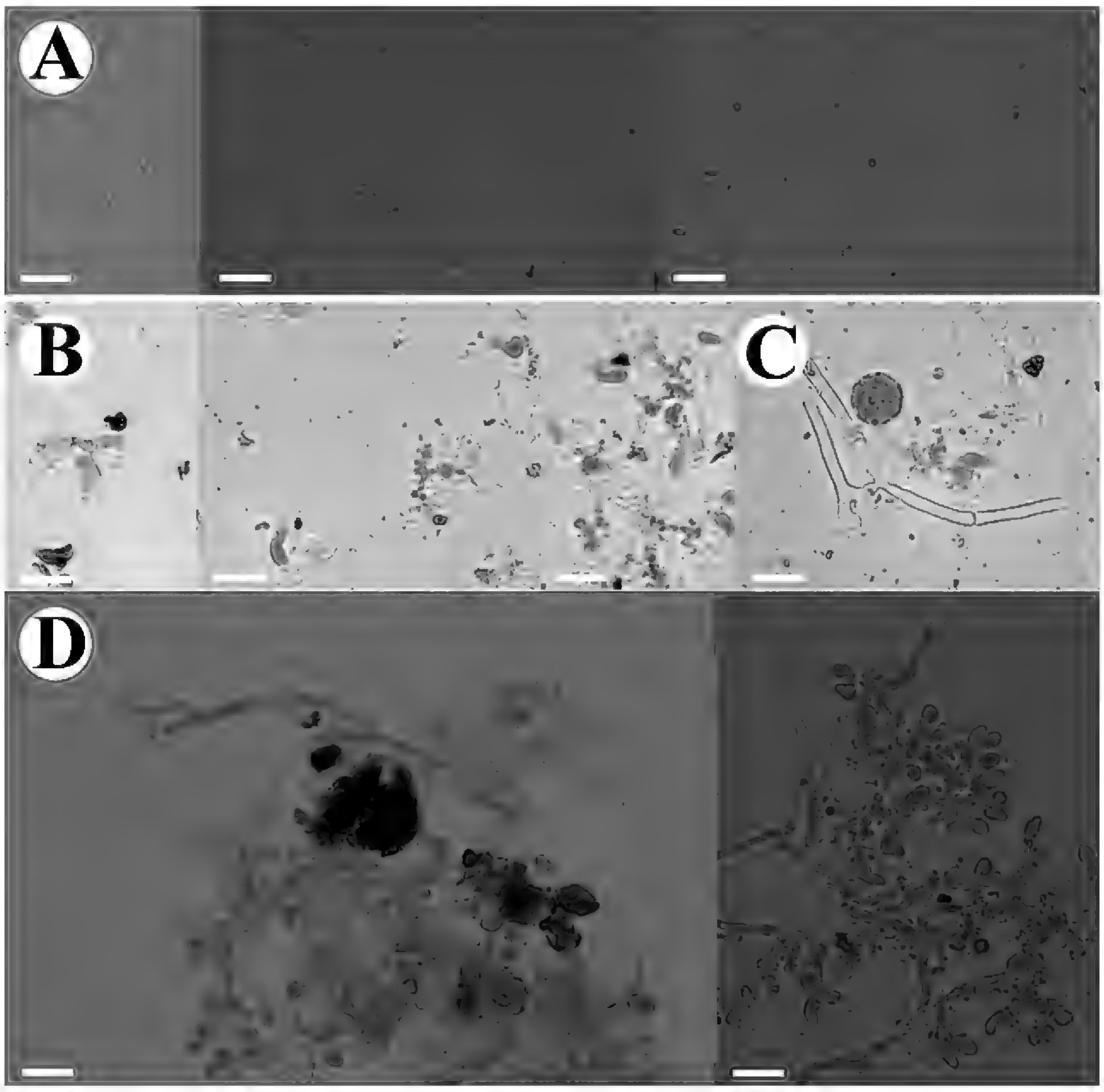


Figure 8. Microscopic structures of *Burgella fissurata* (holotype): basidiospores (**A**), basidia and basidioles; umbrella-shaped cystidia (**B**), generative hyphae (**C**), a section of hymenium (**D**). Scale bars: 10 μm (**A–D**).

***Burgoa wumengshanensis*** **Q. Zhou & C.L. Zhao, sp. nov.**
MycoBank No: 857298
Figs 9–11

**Holotype.** China • Yunnan Province: Zhaotong, Yiliang County, Luozehe Town, Lijiaping Village, Wumengshan National Nature Reserve, GPS coordinates: 27°29'N, 103°55'E, altitude: 1900 m asl., on the fallen branch of angiosperm, leg. C.L. Zhao, 19 September 2023, CLZhao 33227 (SWFC).

**Etymology.** *wumengshanensis* (Lat.): refers to the locality, Wumengshan National Natural Reserve, of the type specimens.

**Description.** Basidiomata annual, resupinate, adnate, pellicular, pruinose upon drying, without odor or taste when fresh, up to 7.4 cm long, 2.1 cm wide, 40–90 µm thick. Hymenial surface smooth, white when fresh, turning to pale cream upon drying. Sterile margin thin, white, up to 1 mm wide.

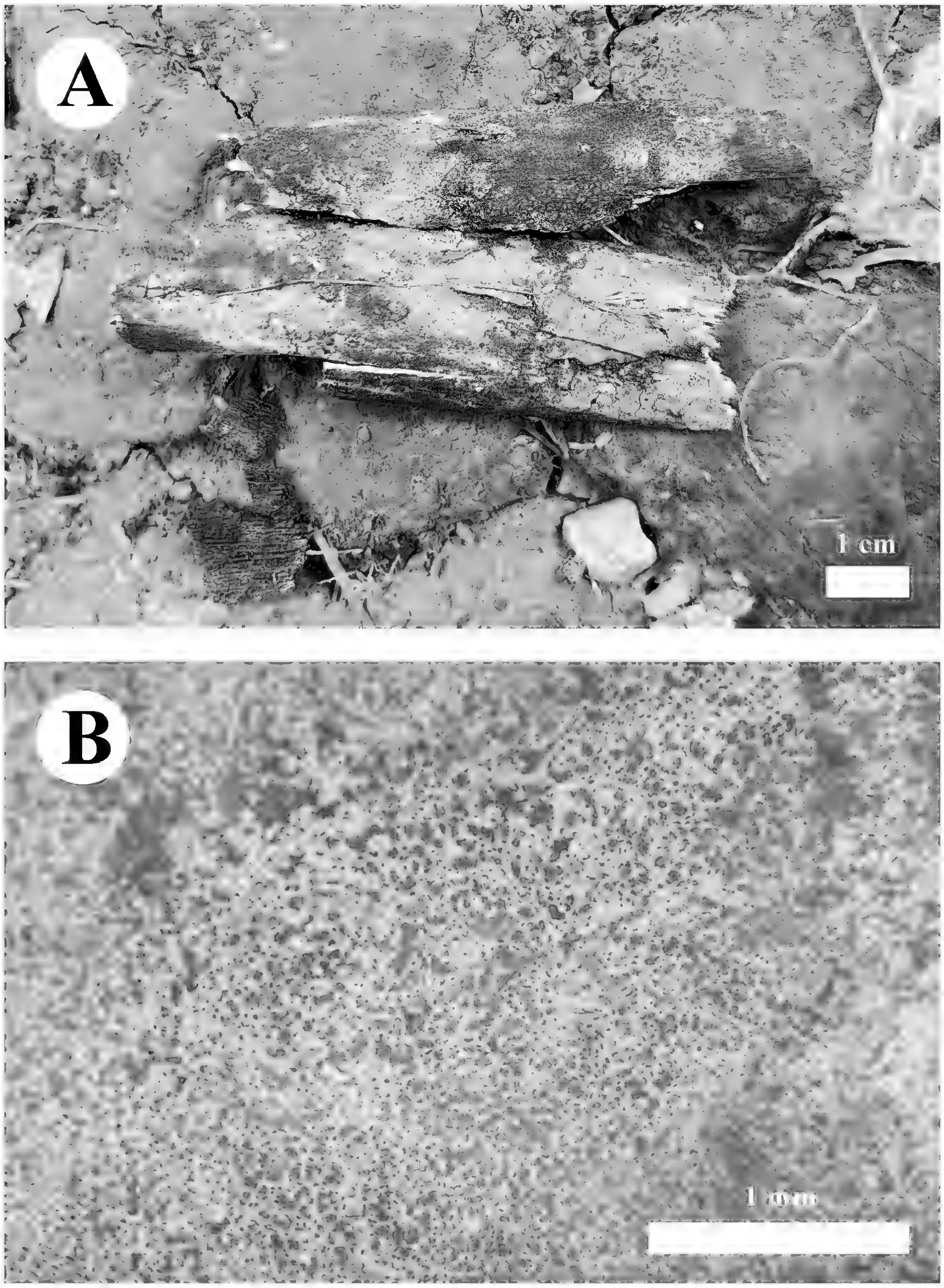


**Figure 9.** Basidiomata of *Burgoa wumengshanensis* (holotype). Scale bars: 1 cm (**A**); 1 mm (**B**)

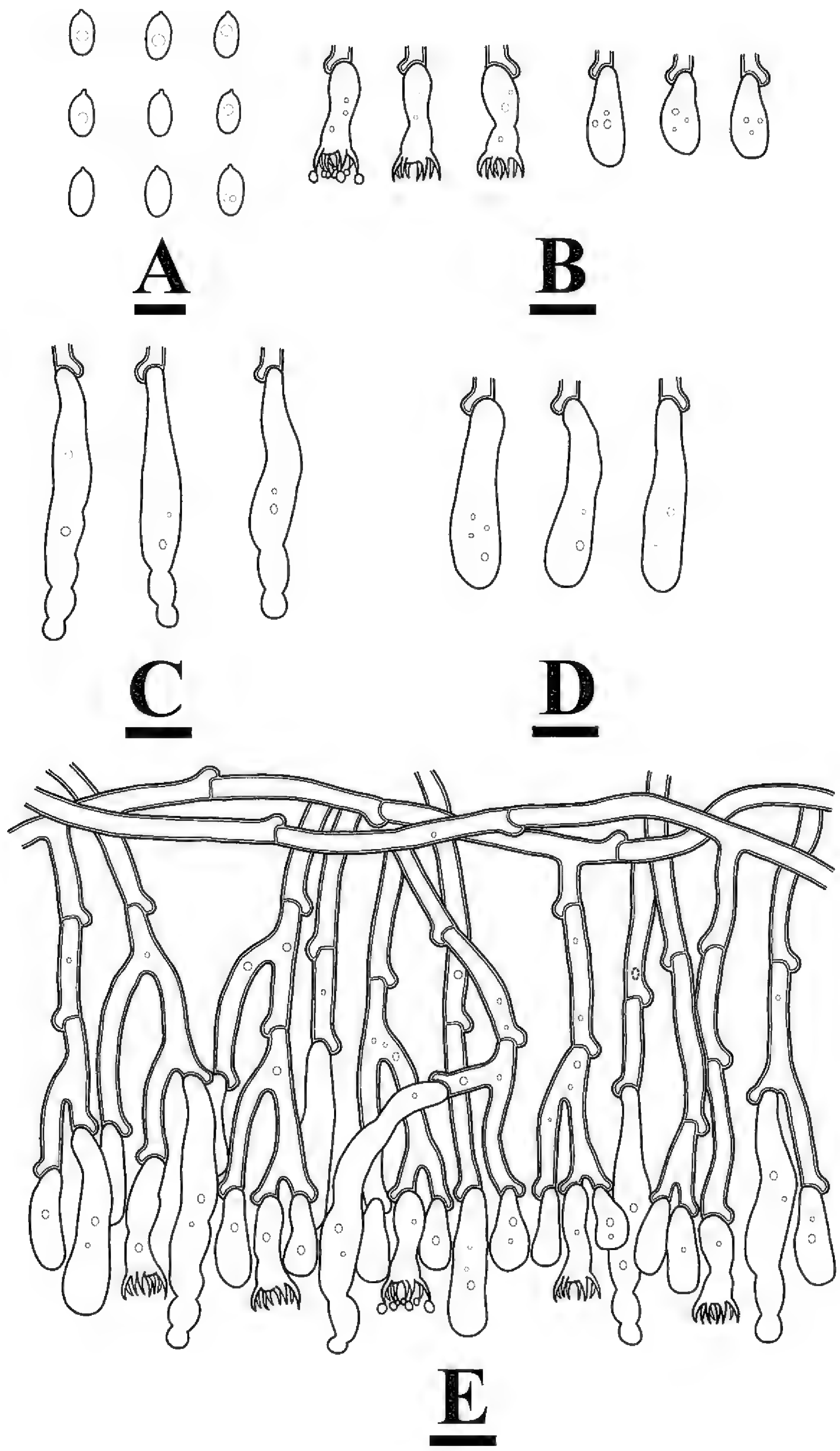


**Figure 10.** Microscopic structures of *Burgoa wumengshanensis* (holotype) basidiospores (**A**), basidia and basidioles (**B**), schizopapillate cystidia (**C**), clavate cystidioles (**D**), a section of hymenium (**E**). Scale bars: 5 μm (**A**), 10 μm (**B, E**).

Hyphal system monomitic, generative hyphae with clamp connections, sometimes with oily contents, colorless, slightly thick-walled, frequently branched, interwoven, 3.5–5 μm in diameter; IKI–, CB–, tissues unchanged in KOH.

Cystidia schizopapillate, colorless, thin-walled, smooth, 30.5–49 × 5.5–8 μm; cystidioles clavate, colorless, thin-walled, smooth, 22–29.5 × 5–8 μm. Basidia urniform, with a median constriction, slightly thick-walled, with 8 sterigmata and a basal clamp connection, 12–20 × 3.5–6 μm; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores ellipsoid, colorless, thin-walled, smooth, with oil drop, IKI–, CB–, (3.5)–4–5.5(–6) × 2–3.5 μm, L = 4.5 μm, W = 2.78 μm, Q = 1.62 (n = 30/1).

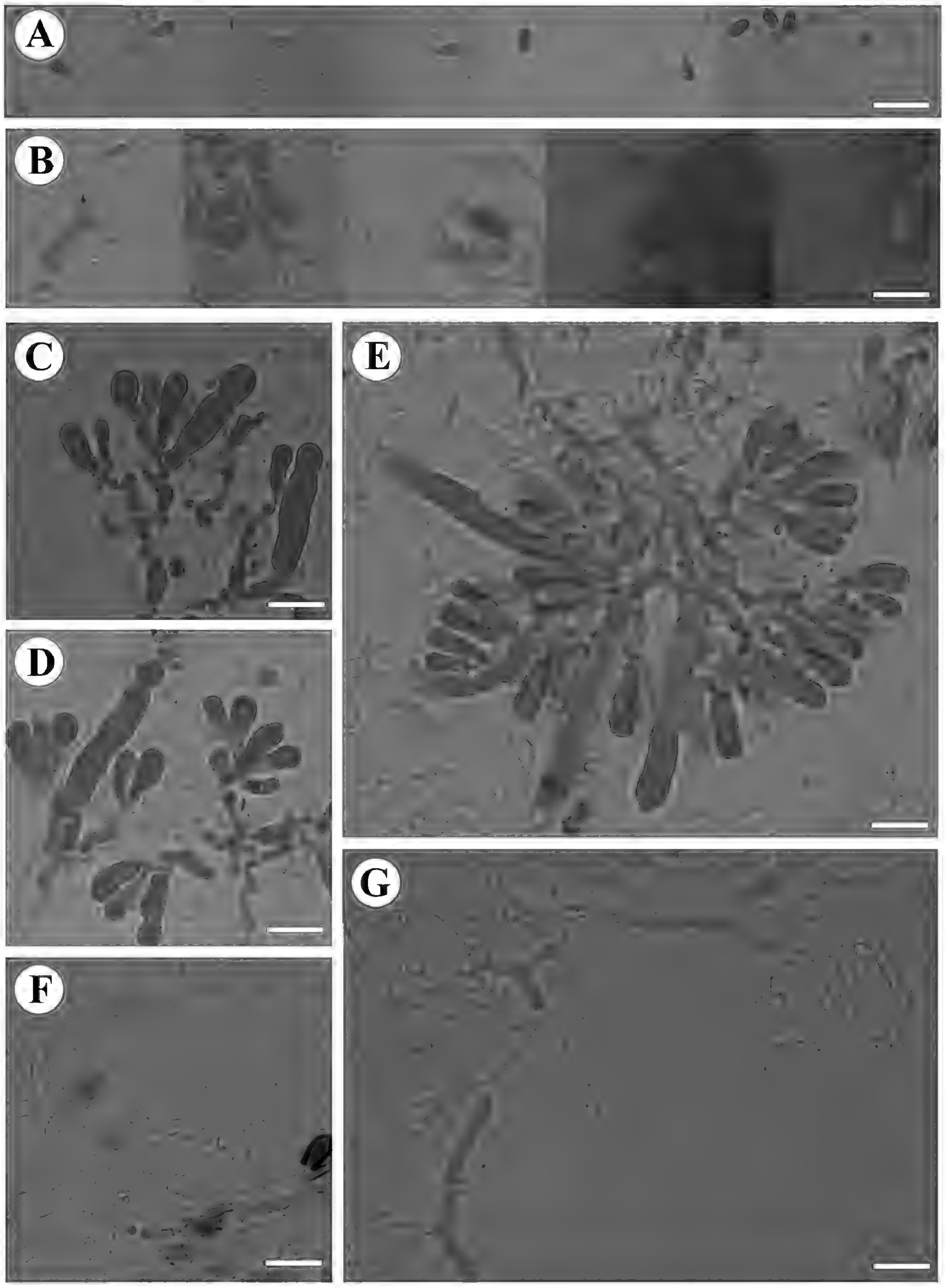


**Figure 11.** Microscopic structures of *Burgoa wumengshanensis* (holotype) basidiospores (**A**), basidia (**B**), clavate cystidioles (**C**), schizopapillate cystidia (**D**), a section of hymenium (**E**), generative hyphae (**F, G**). Scale bars: 10 μm (**A–G**).

***Clavuliella*** **Q. Zhou & C.L. Zhao, gen. nov.**
MycoBank No: 858532

**Type species.** *Clavuliella sinensis* Q. Zhou & C.L. Zhao, sp. nov.

**Etymology.** *Clavuliella* (Lat.): refers to the related genus *Clavulina*.

**Description.** Basidiomata annual, coralloid, gregarious to caespitose clusters, greyish white to light grey when fresh, turning to dark grey upon drying; with sharply acuminate or cristate tips. Hyphal system monomitic, generative hyphae simple-septa, colorless, slightly thick-walled, frequently branched, interwoven. Cystidia and cystidioles absent. Basidia cylindrical, with a median constriction, with 2 sterigmata and a basal simple-septum, with oily contents. Basidiospores subglobose to broadly ellipsoid, colorless, thin-walled, smooth, with oil drop, IKI–, CB–.

**Notes.** In our phylogenetical analyses (Fig. 1), *Clavuliella* was identified as a monophyletic group, typified by *C. sinensis*. The new genus *Clavuliella* falls within the family Hydnaceae (Cantharellales) and is closely related to *Clavulina*. *Clavulina* is distinguished from *Clavuliella* by its clavarioid to coralloid, simple or branched basidiomata with amphigenous hymenia, cylindrical to subclavate basidia with two or more cornuted sterigmata (Schröter 1888; Uehling et al. 2012; He et al. 2019; Gao et al. 2024).

*Clavuliella* resembles *Clavulina* in sharing coralloid basidiomata, subglobose, thin-walled basidiospores. However, *Clavuliella* differs from *Clavulina* by cylindrical basidia, with a median constriction, slightly thick-walled, with 2 sterigmata and a basal simple-septum, with oily contents and simple-septa generative hyphae. In this study, *Clavuliella* originating from the subtropical regions, suggests the possibility of discovering new corticioid taxa through further investigations and molecular analyses.

***Clavuliella sinensis* Q. Zhou & C.L. Zhao, sp. nov.**
MycoBank No: 858533
Figs 12–14

**Holotype.** China • Guizhou Province: Guiyang, Qianlingshan Forest Park, GPS coordinates: 26°36'N, 106°41'E, altitude: 1396 m asl., on the ground, leg. C.L. Zhao, 21 August 2023, CLZhao 31231 (SWFC).

**Etymology.** *sinensis* (Lat.): refers to the type locality (China).

**Description.** Basidiomata annual, coralloid, gregarious to caespitose clusters, 0.6–1.5 cm tall, 0.62–1.6 cm wide, frequently branched 2–3 times, forming dichotomous branches at the apices, without odor or taste, soft when fresh, becoming brittle upon drying, usually lacking obvious basal mycelium; greyish white to light grey when fresh, turning to dark grey upon drying; with sharply acuminate or cristate tips.

Hyphal system monomitic, generative hyphae simple-septa, colorless, slightly thick-walled, frequently branched, interwoven, 4–10.5 µm in diameter; IKI–, CB–, tissues unchanged in KOH.

Cystidia and cystidioles absent. Basidia cylindrical, with a median constriction, slightly thick-walled, with 2 sterigmata and a basal simple-septum, with oily contents, 18.5–43 × 6–9 µm; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores subglobose to broadly ellipsoid, colorless, thin-walled, smooth, with oil drop, IKI–, CB–, (7–)7.5–9.5(–10) × 6.5–8(–8.5) µm, L = 8.52 µm, W = 7.51 µm, Q = 1.13 µm (n = 30/1).

***Sistotrema sinense* Q. Zhou & C.L. Zhao, sp. nov.**
MycoBank No: 857299
Figs 15–17

**Holotype.** China • Yunnan Province: Dali, Weishan County, Qinghua Town, GPS coordinates: 25°01'N, 100°22'E, altitude: 2071.6 m asl., on the fallen branch of angiosperm, leg. C.L. Zhao, 18 October 2022, CLZhao 24876 (SWFC).

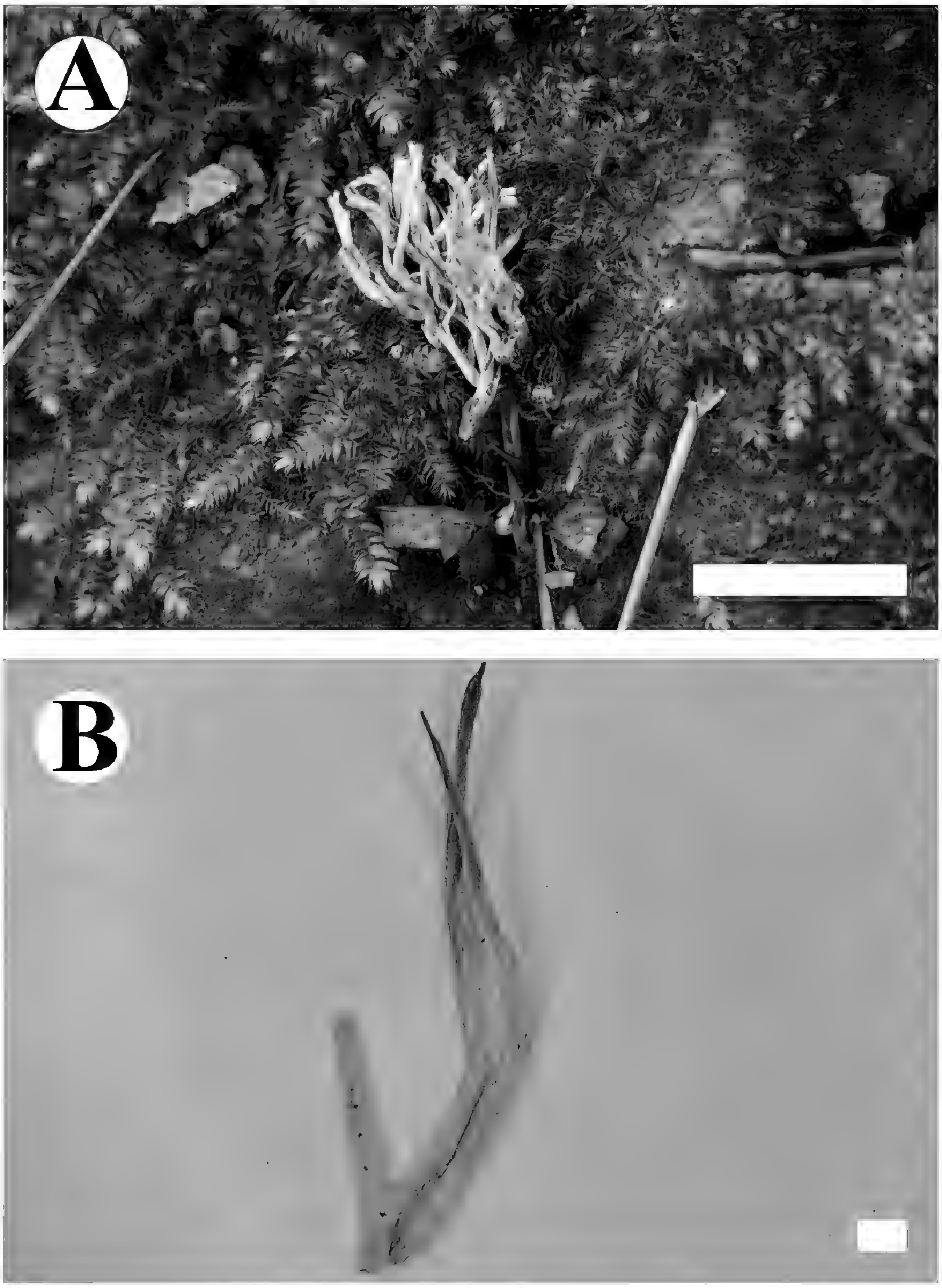


**Figure 12.** Basidiomata of *Clavuliella sinensis* (holotype). Scale bars: 1 cm (**A**); 1 mm (**B**).

**Etymology.** *sinense* (Lat.): refers to the type locality (China).

**Description.** Basidiomata annual, resupinate, adnate, soft coriaceous when fresh, becoming coriaceous upon drying, without odor or taste when fresh, up to 11 cm long, 2.5 cm wide, 50–100 μm thick. Hymenial surface smooth, white when fresh, turning to white to incanus upon drying. Sterile margin thin, white, thinning out, up to 1 mm wide.

Hyphal system monomitic, generative hyphae with clamp connections, often and characteristically with oil content, colorless, slightly thick-walled, frequently branched, interwoven, 2–4 μm in diameter; IKI–, CB–, tissues unchanged in KOH.

Cystidia and cystidioles absent. Basidia suburniform to urniform, slightly thick-walled, with 4 sterigmata and a basal clamp connection, 8–13.5 × 3–5 μm; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores suballantoid to allantoid, colorless, thin-walled, smooth, IKI–, CB–, 3–4.5(–5) × (1–)1.5–2.5 μm L = 3.8 μm, W = 1.72 μm, Q = 2.21 μm (n = 30/1).

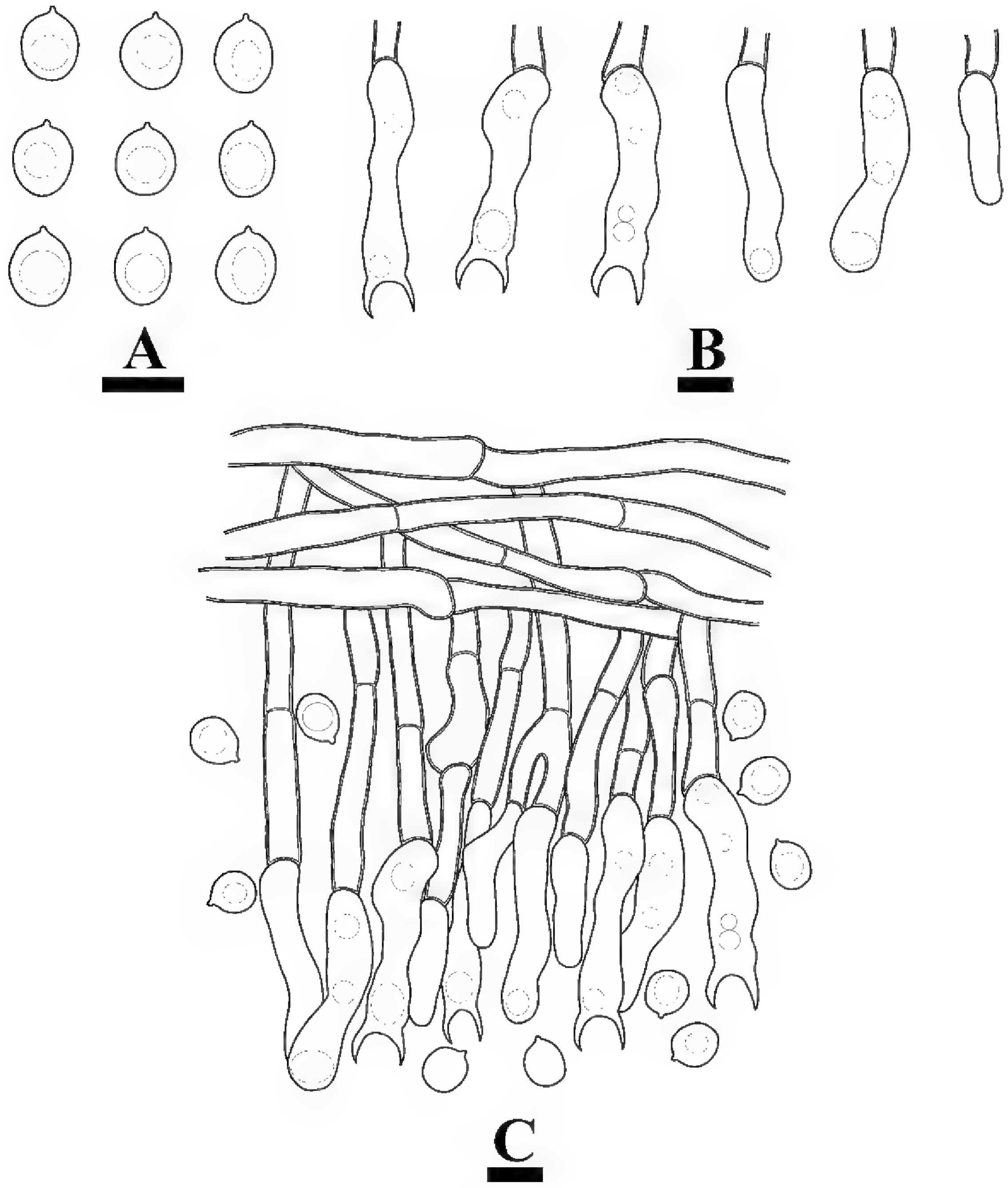


Figure 13. Microscopic structures of *Clavuliella sinensis* (holotype): basidiospores (**A**), basidia and basidioles (**B**), a section of hymenium (**C**). Scale bars: 5 µm (**A**); 10 µm (**B, C**).

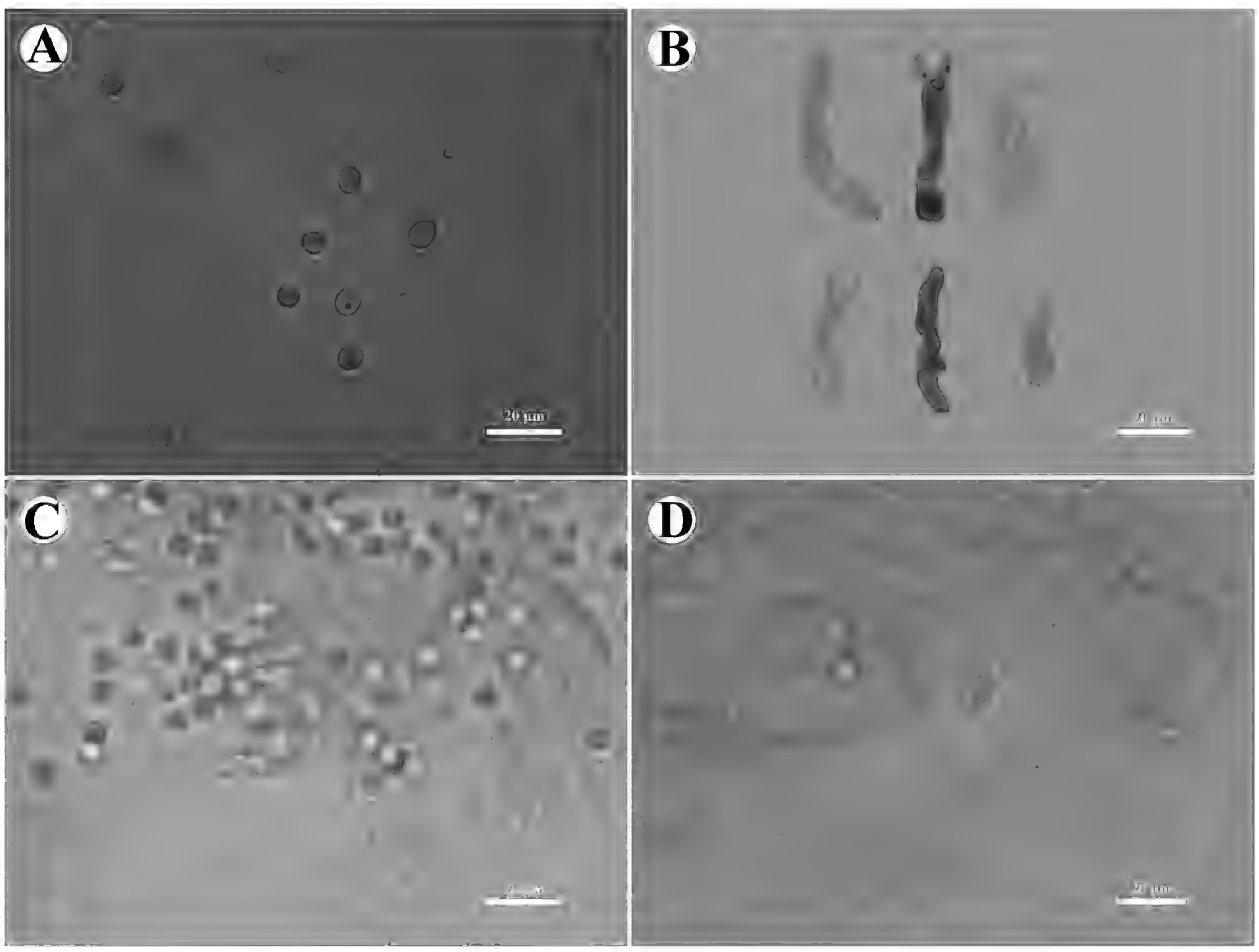


Figure 14. Microscopic structures of *Clavuliella sinensis* (holotype): basidiospores (**A**), basidia and basidioles (**B**), a section of hymenium (**C**), generative hyphae (**D**). Scale bars: 10 µm (**A–D**).

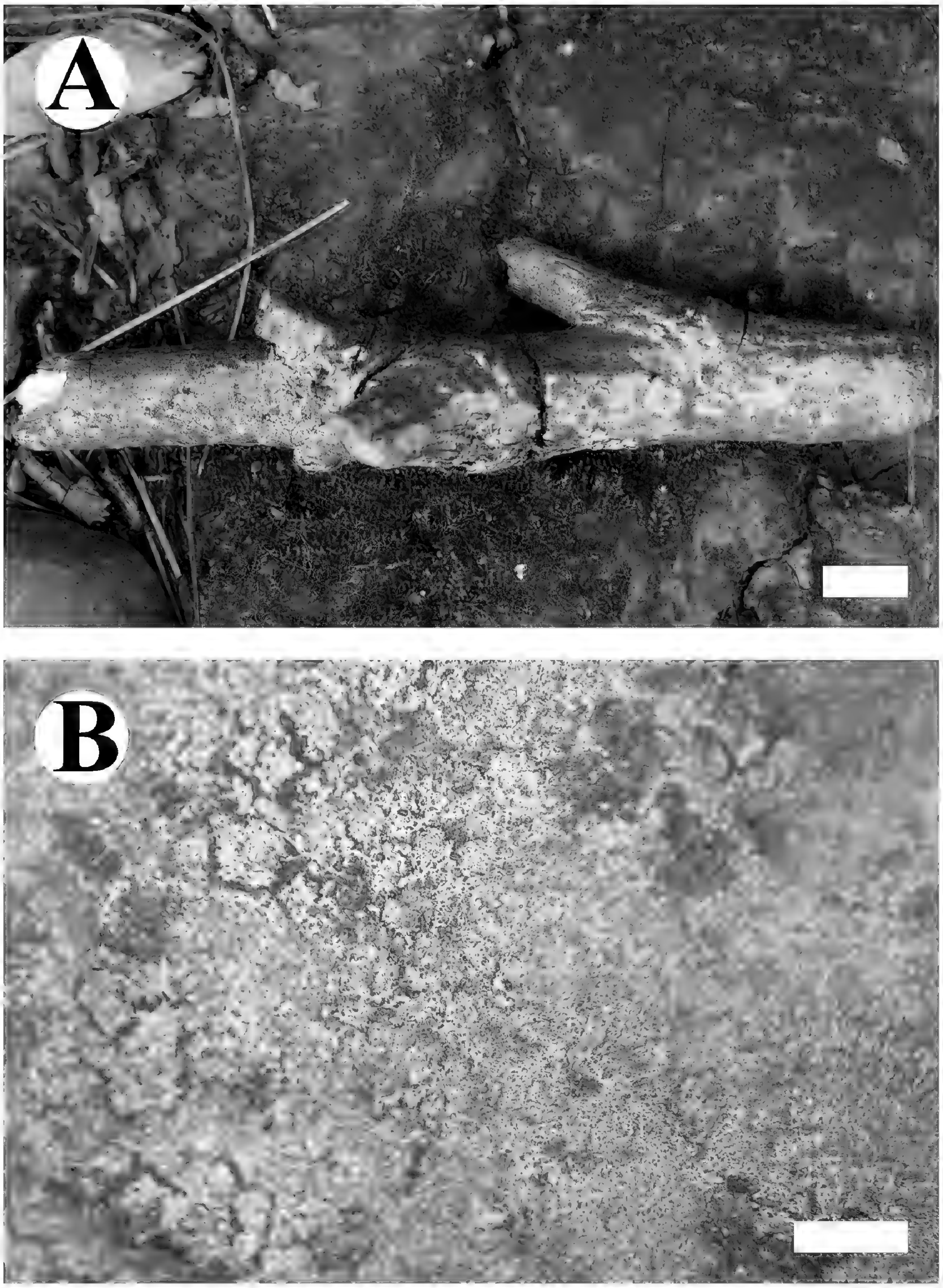


**Figure 15.** Basidiomata of *Sistotrema sinense* (holotype). Scale bars: 1 cm (**A**); 1 mm (**B**).

## Discussion

In recent years, many taxa of wood-inhabiting fungi have been continuously reported and recorded all over the world, including in the genus *Burgella*, *Burgoa*, and *Sistotrema* (Diederich et al. 2014; Koukol and Kubátová 2015; Cai and Zhao 2023; Dong et al. 2024b; Yuan et al. 2024; Zhang et al. 2024; Yang et al. 2025). Several previous studies, based on ITS+nLSU sequence data, confirmed phylogenetic relationships, in which the genus *Burgella*, *Burgoa*, *Clavuliella*, and *Sistotrema* are nested in the order Cantharellales (Diederich et al. 2014; Koukol and Kubátová 2015).

Phylogenetically, based on the multiple loci in the family Hydnaceae, four genera; *Burgella*, *Burgoa*, *Clavuliella*, and *Sistotrema* were located in this family (Zhou and Qin 2013; Vu et al. 2019; Masumoto and Degawa 2020; Sugawara et al. 2022;

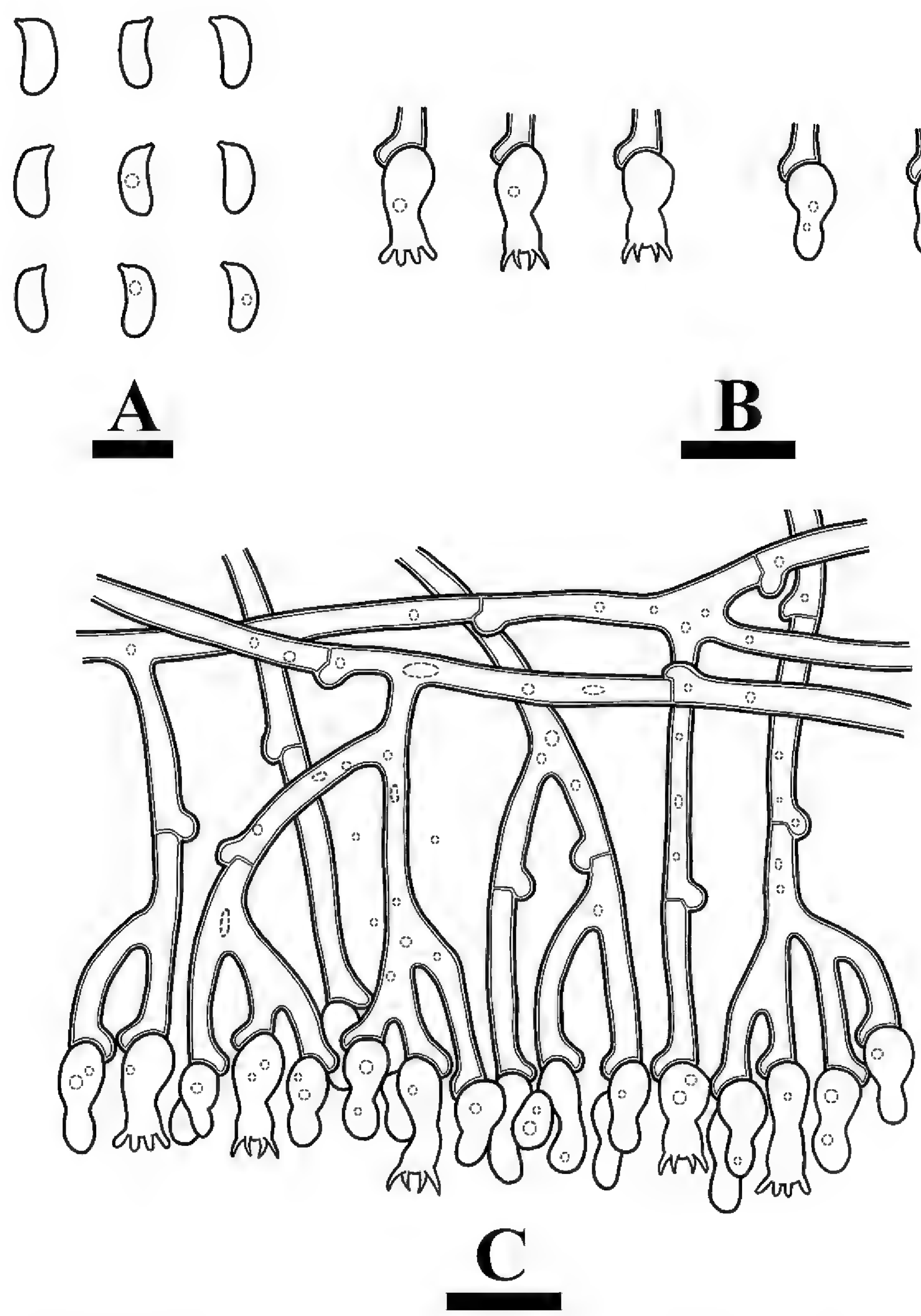


**Figure 16.** Microscopic structures of *Sistotrema sinense* (holotype): basidiospores (**A**), basidia and basidioles (**B**), a section of hymenium (**C**). Scale bars: 5 µm (**A**); 10 µm (**B, C**).

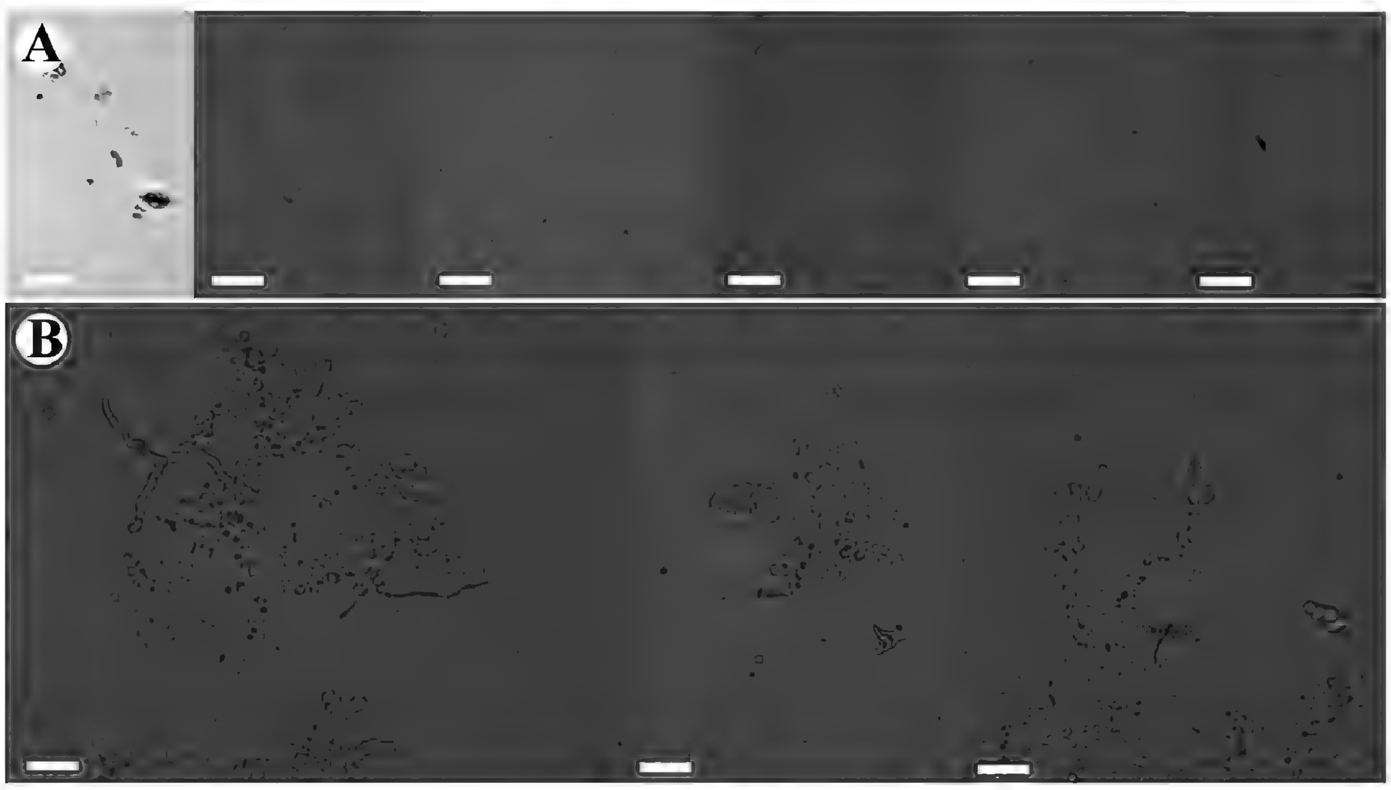


**Figure 17.** Microscopic structures of *Sistotrema sinense* (holotype): basidiospores (**A**), a section of hymenium (**B**). Scale bars: 10 µm (**A, B**).

Campo et al. 2023; Cai and Zhao 2023). In the present study, based on the phylogram inferred from the ITS+nLSU data (Fig. 1), two new species were grouped into the genus *Burgella*, in which *B. albofarinacea* was closely related to *B. flavoparmeliae* and *B. fissurata* was grouped with *B. lutea*. The phylogram based on inferences from the ITS and nLSU data (Fig. 1) showed that *B. wumengshanensis* clustered into the genus *Burgoa*, in which it was grouped closely with *B. anomala* and *B. verzuoliana*. The phylogram based on inferences from the ITS and nLSU data (Fig. 1) showed that *Clavuliella* was identified as a monophyletic group, typified by *C. sinensis*, in which it was grouped closely with *C. minor* X.X. Huang & L.H. Qiu, *C. cristata*, and *C. iris* Loizides, Bellanger & P.-A. Moreau. The phylogenetic tree (Fig. 2), inferred from the ITS+nLSU sequences, highlighted that *Sistotrema sinense* was grouped closely with *S. brinkmannii* and *S. farinaceum*.

Morphologically, *Burgella flavoparmeliae*, *B. lutea* and *B. fissurata* are similar to *B. albofarinacea* by having the generative hyphae with septa or with clamp connections. (Diederich and Lawrey 2007). However, *B. flavoparmeliae* differs from *B. albofarinacea* by the irregularly shaped, coralloid, orange agglomerations of bulbils and generative hyphae with septa or without clamp connections, with both morphologies present on the same hyphae at neighboring septa (Diederich and Lawrey 2007). *B. lutea* is distinguished from *B. fissurata* by the superficial, yellow to orange-yellow, roundish bulbils (Diederich et al. 2014). *B. fissurata* is distinguishable from *B. albofarinacea* by the pruinose hypochnoid hymenial surface, with umbrella-shaped cystidia, basidia with 4 sterigmata, and its smaller basidia (6–11.5 × 2–4.5 μm; Diederich and Lawrey 2007; Koukol and Kubátová 2015; Kiyuna et al. 2015).

*Burgella flavoparmeliae* is separated from *B. fissurata* by the irregularly shaped, coralloid, orange agglomerations of bulbils and generative hyphae with septa or without clamp connections, both situations present on the same hyphae at neighbouring septa (Diederich and Lawrey 2007). *B. lutea* is distinguished from *B. fissurata* by the superficial, yellow to orange-yellow, roundish bulbils (Diederich et al. 2014). *B. albofarinacea* differs from *B. fissurata* by the pellicular, coriaceous hymenial surface, bigger basidia with 8 sterigmata and bigger basidiospores (Cai and Zhao 2023).

Morphologically, *Burgoa anomala* and *B. verzuoliana* are similar to *B. wumengshanensis* by having the generative hyphae with clamp connections (Koukol and Kubátová 2015). However, *B. anomala* is distinguishable from *B. wumengshanensis* by having spherical bulbils, and hyaline to pale brown generative hyphae, thin-walled, thinner (2–5 μm) in diameter (Koukol and Kubátová 2015); *B. verzuoliana* is distinguished from *B. wumengshanensis* by having spherical bulbils (Diederich and Lawrey 2007).

Morphologically, *Clavulina cristata*, *C. griseoviolacea* Yue Gao, Hao Zhou, & C.L. Hou, and *C. pallida* Yue Gao, Hao Zhou & C.L. Hou are similar to *Clavuliella sinensis* by having clavarioid to coralloid basidiomata and guttulate basidiospores (Uehling et al. 2012; Gao et al. 2024). However, *Clavulina cristata* is separated from *Clavuliella sinensis* by having cylindrical to subclavate basidia with two or more cornuted sterigmata (Gao et al. 2024); *Clavulina griseoviolacea* differs from *Clavuliella sinensis* by having gray to dark grayish violet basidiomata with a white stipe, hyphae with clamp connections, and smaller basidiospores (6.5–8.0 × 6.2–7.2 μm; Crous et al. 2014); *Clavulina pallida* is distinguishable from *Clavuliella sinensis* by having solitary or scattered basidi-

omata, generative hyphae clamp connections, and longer basidia (34.2–48.5 × 4.8–6.3 μm; Gao et al. 2024).

Morphologically, *Sistotrema diademiferum* (Bourdot & Galzin) Donk, *S. coroniferum* (Höhn. & Litsch.) Donk and *S. hispanicum* M. Dueñas, Ryvarden & Tellería are similar to *S. sinense* by having the urniform basidia and basal hyphae with clamp connections (Bernicchia and Gorjón 2010). However, *S. diademiferum* is separated from *S. sinense* by the smooth, porulose hymenophore, larger basidia with 6 sterigmata (15–20 × 5–7 μm), and ovoid to subglobose basidiospores (Bernicchia and Gorjón 2010). *S. coroniferum* is distinguishable from *S. sinense* by the smooth hymenophore, with gloeocystidia, basidia with 6 sterigmata, and longer subcylindrical basidiospores (5–6 × 2–2.5 μm; Bernicchia and Gorjón 2010). *S. hispanicum* differs from *S. sinense* by the whitish to yellow hymenial surface and bigger narrowly ellipsoid to subreniform basidiospores (5.5–6 × 3–4 μm; Bernicchia and Gorjón 2010).

As wood-inhabiting fungi efficiently degrade lignocellulose in wood, they play a crucial ecological role in material recycling and energy flow in forest ecosystems, as well as playing a major economic role (Sugawara et al. 2022; Zhang et al. 2022; Bondartseva and Zmitrovich 2023; Campo et al. 2023; Cui et al. 2019; Gao et al. 2024; Liu et al. 2023a, b; Sun et al. 2020; Sun et al. 2022; Ji et al. 2022). Wood-inhabiting fungi are an extensively studied group of Basidiomycota, but their diversity is still not well known in China, and many recently described taxa in this ecological group have been discovered from China (Sugawara et al. 2022; Cai and Zhao 2023; Wang et al. 2023; Wang et al. 2024; Wu et al. 2022; Yuan et al. 2023; Zhao et al. 2024). Four new species and a new genus, from the Yunnan and Guizhou Provinces of China, serve as examples of the understudied fungal diversity present in the P.R. of China.. On a wider scale, this study enriches our knowledge on the diversity of wood-inhabiting fungi worldwide.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: CZ. Methodology: CZ and QZ. Software: CZ, QZ, and HZ. Validation: CZ and QZ. Formal analysis: CZ and QZ. Investigation: CZ, CQ, CZ, QS, SZ, NM, TX, and QZ. Resources: CZ. Writing – original draft preparation: CZ, CQ, CZ, QS, YL, SZ, NM, TX,

HZ, and QZ. Writing – review and editing: CZ and QZ. Visualization: CZ and QZ. Supervision: CZ and QZ. Project administration: CZ. Funding acquisition: CZ. All authors have read and agreed to the published version of the manuscript.

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## Data availability

All of the data that support the findings of this study are available in the main text.

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